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Maximum Tolerable Level, Digestion, and Metabolism of D-Glucose (Cerelose) in Rainbow Trout (*Salmo gairdneri*) Reared on a Practical Trout Diet

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HILTON, J. W., J. L. ATKINSON, AND S. J. SLINGER. 1982. Maximum tolerable level, digestion, and metabolism of D-glucose (cerelose) in rainbow trout (*Salmo gairdneri*) reared on a practical trout diet. Can. J. Fish. Aquat. Sci. 39: 1229–1234.

The maximum tolerable dietary level, digestion, and metabolism of D-glucose (cerelose) were investigated in rainbow trout (*Salmo gairdneri*) reared on practical diets containing optimum protein and lipid levels at two different water temperatures for 12 wk. Liver glycogen levels (LG) and liver:body weight ratios (LB) initially increased with increasing dietary glucose, but leveled off above 10–15% glucose. The plateauing of LB and LG was consistent with the plateauing of liver glucose-6-phosphate dehydrogenase activity (G6PD) and probably overall hexose monophosphate shunt (HMS) activity at high dietary levels of glucose. This indicates that there may be an optimum ratio of digestible carbohydrate to lipid in salmonid diets. LG and LB tended to be higher in trout reared upon the same dietary glucose level in fish reared at 11°C as compared with those at 15°C. This may have been caused by increased activity of the HMS as indicated by increased activity of liver G6PD in fish acclimated to 11°C as compared to trout reared at 15°C on the same dietary glucose level (when assayed at 15°C). The digestion coefficient of glucose was uniformly high (96–99%) and not affected by either dietary glucose level (up to 25% of the diet) or water temperature (11 or 15°C). The maximum tolerable level of glucose in salmonid diets appears to be dependent upon the protein, lipid, and overall energy content of the diet.

Key words: trout, glucose digestion, glucose metabolism, maximum tolerable levels, water temperature, dietary energy

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On a étudié le niveau de diète tolérable maximal, la digestion et le métabolisme du D-glucose (cérelose) chez des truites arc-en-ciel (*Salmo gairdneri*) élevées à des diètes pratiques contenant des niveaux optima de protéines et de lipides à deux températures de l'eau

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différentes pendant 12 semaines. Les niveaux de glycogène hépatique (LG) et les rapports foie/poids corporel (LB) augmentent au début en même temps que le glucose alimentaire, mais atteignent un palier au-delà d'environ 10 à 15 % de glucose. Cet arrêt de LB et de LG s'accorde avec celui de l'activité de la glucose-6-phosphate déshydrogénase hépatique (G6PD) et probablement avec l'arrêt de l'activité générale de shunt du monophosphate hexose (SMH) à de hauts niveaux de glucose dans le régime. Il y a donc, d'après ces résultats, un rapport optimal hydrates de carbone/lipides digestibles dans les diètes des salmonidés. LG et LB ont tendance à être plus élevés chez des truites nourries au même niveau de glucose mais à 11°C au lieu de 15°C. Ceci peut être le résultat d'une activité accrue du SMH, comme l'indique une plus grande activité de la G6PD hépatique chez des poissons acclimatés à 11°C comparativement aux truites élevées à 15°C et au même niveau de glucose alimentaire (tests à 15°C). Le coefficient de digestion du glucose est uniformément élevé (96−99 %) et n'est influencé ni par le niveau de glucose alimentaire (jusqu'à 25 %) du régime, ni par la température de l'eau (11 ou 15°C). Le niveau tolérable maximal de glucose dans le régime alimentaire des salmonidés semble dépendre de la teneur en protéines et en lipides, et du contenu énergétique total du régime.

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RECENT research in our laboratory (Hilton and Atkinson 1982) indicated that the optimum level of digestible carbohydrate (cerelose, D-glucose) in isocaloric and isonitrogenous practical diets for rainbow trout (*Salmo gairdneri*) is ~ 14% of the diet. This agrees favorably with the results of Phillips et al. (1948) but is in contrast to the results of Buhler and Halver (1961), Luquet (1971), and Bergot (1979). These latter researchers noted that the optimum level of digestible carbohydrate in salmonid diets varied between 20 and 30% of the diet. While the reasons for this diversity are still unclear, it is possible that differences in fish species, diet composition, digestibility of the carbohydrate added, and water temperature used in these studies are major factors. Takeuchi et al. (1978) have concluded that the optimum levels of protein and lipid, the preferred dietary energy sources of trout, are ~ 35% and 15−20%, respectively. This conclusion was verified by a study of Reinitz et al. (1978) using a practical trout diet. It seems likely that different proportions of protein and fat would alter carbohydrate metabolism and both the maximum tolerable level and optimum level of carbohydrate inclusion.

It is possible that the level of dietary carbohydrate affects its digestibility by rainbow trout, as reported by Takeuchi et al. (1979) in studies on carp. Water temperature also appears to affect carbohydrate metabolism in salmonids, causing an increased glycogen infiltration of the liver at low water temperatures (NRC 1973). It is thus possible then that both the maximum and optimum level of dietary carbohydrate may be affected by water temperature in salmonids.

This study on rainbow trout was conducted to determine: (1) the maximum tolerable level of D-glucose (cerelose) in practical diets containing optimum levels of protein, lipid, and energy; (2) the effect of the level of inclusion of glucose on its digestibility in practical diets; and (3) the effect of water temperature on the availability and maximum tolerable level of inclusion of glucose in practical diets.

Materials and Methods

General Design

Practical trout diets containing from 0 to 25% glucose were fed to duplicate groups of juvenile rainbow trout reared at 11 and 15°C for 12 wk. After 12 wk the weight gain, feed-efficiency, digestibility of glucose, and other physiological parameters were determined in the trout.

Diet Preparation

Six practical trout diets with increasing levels of D-glucose (cerelose) were formulated (Table 1) and processed by steam pelleting in a California pellet mill (San Francisco, CA, USA). Proximate analysis of the diets for ash, moisture, and protein was performed as described by Horwitz et al. (1970) and the lipid content determined by the method of Bligh and Dyer (1959). The glucose content of the diets was determined by homogenizing 100 mg of diet with 10 mL of distilled water in a Polytron mixer (Brinkman Instruments, Rexdale, Ont.). The homogenate was then centrifuged and the glucose content of the supernatant determined by the glucose oxidase method (Glucose Kit No. 510, Sigma Chemical Co. St. Louis, MO). Diet samples spiked with known concentrations of glucose indicated that the percent recoveries of glucose by this method were 106 ± 4% (mean ± standard deviation of six samples).

Supply and Maintenance of Fish

Rainbow trout were obtained from the Ontario Ministry of Natural Resources, Normandale Hatchery, Turkey Point, Ont. After a 2-wk acclimation period, ~ 70 fish per tank (mean weight 3.1 ± 0.1 g/fish) were transferred to two 12-tank systems. One system comprised rectangular enamel-lined metal tanks (capacity 45 L) maintained at 15.4 ± 0.3°C. The other system involved the use of rectangular Fiberglass tanks (capacity 60 L) and was maintained at 11.0 ± 1.0°C. The tanks were aerated and maintained on a one-pass water system which had a flow rate of 2−3 L per minute. The pH varied between 7.4 and 7.8 and dissolved oxygen ranged from 7.1 to 8.4 $mg \cdot L^{-1}$ in the two systems throughout the study. The test diets were fed to duplicate groups of ~ 70 fish per tank per system for 12 wk. The fish were fed 3−4 times per day and the size of feed particle was adjusted after each 28-d

TABLE 1. Composition and analysis of the test diets (results are the mean of three to four samples).

Ingredient	Diet number 1	2	3	4	5	6
			(%)			
Capelin meal	35	35	35	35	35	35
Soybean meal	20	20	20	20	20	20
Wheat middlings	7	7	7	7	7	7
Cerelose	0	5	10	15	20	25
Alpha-floc	25	20	15	10	5	0
Vitamin Pre-Mix[a]	2	2	2	2	2	2
Mineral Pre-Mix[a]	1	1	1	1	1	1
Salmon oil	10	10	10	10	10	10
			Analysis			
Protein	34.8	35.4	35.6	35.9	35.2	35.4
Lipid	17.5	17.6	17.4	17.4	17.7	17.4
Ash	5.2	5.9	5.6	5.8	6.2	5.9
Moisture	6.1	6.4	6.7	6.9	7.9	7.3
Glucose	0.7	3.9	9.9	13.2	18.0	24.1

[a]Vitamin and Mineral Pre-Mix as given in Cho et al. 1976.

period. The fish were fed to satiety as described by Hilton and Slinger (1981).

GROWTH AND BIOCHEMICAL ASSAYS

Body weights, feed-gain ratios, and total mortalities were determined after each 28-d period. After 12 wk, 30 fish were randomly selected from each tank and individually weighed; their livers were dissected out, weighed, immediately frozen with liquid nitrogen, and stored at −20°C until required for analysis. The livers were assayed for glycogen content by the method of Murat and Serafty (1974). Carcass samples were collected from each tank, freeze-dried, and stored at −20°C. The carcass ash (ignition at 600°C), moisture (weight loss at 105°C for 24 h), and protein content (N × 6.25) were determined as described by Horwitz et al. (1970), and the carcass lipid by the method of Bligh and Dyer (1959).

Blood was collected from four to eight fish (fasted 18 h) per tank in heparinized centrifuge tubes after transection of the caudal peduncle, immediately centrifuged at 3500 × *g* for 5 min, and the plasma stored at −20°C until required for analysis. Plasma glucose was determined by the glucose oxidase method (Glucose Kit No. 510, Sigma Chemical Co. St. Louis, MO) and plasma protein by the method of Lowry et al. (1951).

Enzyme activities were determined in crude liver extracts from fish which had received the various diets for at least 12 wk. Four to six fish were randomly sampled from each tank, individually weighed, and the livers dissected and weighed. Livers were homogenized and the crude supernatant extract prepared and assayed for glucose-6-phosphate dehydrogenase (EC 1.1.1.49; G6PD) activity as described by Freedland (1967) and pyruvate kinase (EC 2.7.1.40; PK) activity by the method of Pogson (1968). All assays were performed at 15°C using a Gilford recording spectrophotometer equipped with a thermoset temperature controlled cuvette system (Gilford Instrument Laboratories Inc., Oberlin, OH). Body and liver weights were determined for the fish sampled and enzyme activities expressed in units per 100 grams body weight.

DIGESTIBILITY COEFFICIENT OF CERELOSE

Following the 12-wk test period, trout were fed the same test diets containing 1% chromic oxide (Fisher Chemical Co., Toronto, Ont.) for a period of 1−2 wk. Sixteen to 20 h after feeding, fifty fish per tank were killed and their gastrointestinal tracts removed. Fecal samples were then obtained from the rectum and pooled to make up to two fecal samples per tank of ~ 20 to 30 fish feces per sample. The samples were then frozen at −20°C, freeze-dried, and stored for analysis.

Samples of test diets and feces were analyzed for chromium by atomic absorption spectrophotometry (Arthur 1970), and moisture and glucose content as previously described.

The apparent glucose digestibility coefficient (DCC) was calculated using the following formula:

$$\text{DCC} = 100 - \left[100\left(\frac{\%\text{ chromic oxide feed}}{\%\text{ chromic oxide feces}}\right) \times \left(\frac{\%\text{ glucose in feces}}{\%\text{ glucose in feed}}\right)\right].$$

STATISTICAL ANALYSIS

The results were subjected to either linear regression or analyses of variance, and where appropriate differences determined at the 5% level using Tukey's procedure as described by Steel and Torrie (1960).

Results

GROWTH, CARCASS, AND LIVER COMPOSITION

After 12 wk, there was no significant difference (by linear regression) in the growth or mortality (Table 2), or the proximate analysis of the carcasses from the different groups of trout reared at 11 or 15°C (Table 3).

Liver:body weight ratios (LB) increased with increasing glucose up to 15% of the diet (dietary group 4, Table 4). Above 15% dietary glucose, no further increase in LB was detected at either 11 or 15°C. Similarly liver glycogen content (LG) also increased with increasing dietary glucose, but leveled off above 10% glucose (group 3). Both LB and LG tended to be slightly higher at 11°C than at 15°C in trout fed the same level of dietary glucose.

GLUCOSE DIGESTIBILITY−PLASMA COMPOSITION

The digestion of glucose was high in all groups of trout, varying between 95.7 and 99.1% at 11°C, and 97.1 and 99.4% at 15°C. No significant difference was detected in either the plasma glucose or plasma protein content of the different groups of trout reared at either 11 or 15°C (Table 5).

ENZYME ACTIVITIES

Both hepatic G6PD and PK activity tended to increase

TABLE 2. Growth performance of the rainbow trout after 12 wk on the diets at 15 and 11.5°C (results are the mean of two groups per treatment ± standard deviation).

	Temp. °C	Diet number 1	2	3	4	5	6
Weight gain (kg/100 fish)[a]	15	3.3±0.1	3.1±0.1	3.1±0.1	3.1±0.1	3.0±0.3	3.1±0.1
	11	1.8±0.1	1.8±0.1	1.9±0.1	1.8±0.3	1.9±0.1	1.6±0.2
Feed: gain[a] ratio	15	1.1±0.2	1.1±0.1	1.1±0.2	1.1±0.2	1.1±0.2	1.1±0.2
	11	1.4±0.2	1.2±0.3	1.3±0.2	1.4±0.2	1.3±0.2	1.5±0.2
Mortalities[b]	15	0	0	1.2	2.8	2.8	0
	11	1.5	2.8	2.2	1.5	1.5	0

[a]Initial body weight 3.1 ± 0.1 g/fish.
[b]Number of mortalities per 10 000 fish days.

TABLE 3. The carcass proximate analysis of trout after 12 wk on the test diets. (Results based upon the mean of four pooled samples (four to six fish per sample).)

Analysis	Temp. °C	Diet number 1	2	3	4	5	6
				(%)			
Protein	15	44.7	41.0	44.0	42.8	43.0	45.1
	11	47.7	47.1	45.2	45.4	46.6	47.5
Lipid	15	43.9	44.0	43.0	44.0	43.9	42.9
	11	42.1	42.6	44.6	45.5	42.8	43.7
Ash	15	6.3	7.1	6.3	6.1	7.4	6.0
	11	6.2	6.1	6.3	6.3	6.6	6.1
Dry matter	15	31.6	31.4	30.6	31.4	31.3	31.1
	11	30.7	30.4	31.1	30.9	30.2	30.8
Energy (kJ/g)	15	28.0	28.1	28.0	27.8	27.7	27.8
	11	28.1	27.8	28.6	28.5	28.3	28.3

progressively with increasing levels of dietary glucose in the trout reared at 15°C (Table 6). In contrast, when the fish were reared at 11°C both enzymes tended to level off in activity at higher glucose levels (above 20% inclusion (group 5) for G6PD, and above 15% inclusion (group 4) for PK. However, because of the variability of enzyme activity within treatments, G6PD was significantly higher only at the 25% glucose level at 15°C and the 20% glucose level at 11°C, and PK activity was not significantly different even at these high levels. When assayed at 15°C, both G6PD and PK activity tended to be higher in trout reared at 11°C compared to 15°C with the same level of glucose except at the highest level of inclusion (group 6).

Discussion

The maximum tolerable level of digestible carbohydrate is the level that can be efficiently digested and metabolized by the fish without causing any growth impairment or increase in mortality rate. In contrast the optimum level of digestible carbohydrate is the level that cannot only be efficiently digested and metabolized but also efficiently utilized as an energy source by the fish. On the basis of the growth parameters (Table 2), the digestibility coefficients of glucose (Table 5), and the plasma glucose and protein levels (Table 6), the maximum tolerable level of digestible carbohydrate may be in excess of 25% of the diet for rainbow trout. This is higher than the level of ~ 14% determined to be the optimum for digestible carbohydrate inclusion from previous research in our laboratory (Hilton and Atkinson 1982). The two studies are not directly comparable, as the energy level and source of energy used differ markedly. In the study of Hilton and Atkinson (1982), the test diets were theoretically isocaloric and differed only in the proportions of carbohydrate and lipid.

In the present study, optimal levels of protein, lipid, and energy were available in the diets prior to supplementation with glucose. The growth and feed efficiency data (Table 2) showed that glucose was of no more value in these diets than cellulose which has been found in our laboratory to be totally indigestible by the trout (Hilton et al. unpublished observations). Therefore, glucose was probably not being utilized efficiently as an energy source. Similarly, in the studies of Luquet (1971) and Bergot (1979), the higher levels of the preferred energy sources (protein and lipid) in their diets would be expected to influence the determination of the maximum tolerable and of the optimal level of digestible carbohydrate, and presumably account at least in part for their high estimates compared to those of Phillips et al. (1948) and Hilton and Atkinson (1982). In the case of the study by Buhler and Halver (1961), the semipurified test diet used was imbalanced in a number of nutrients, thus precluding a clear interpretation of their results. Thus the optimum and maximum tolerable levels of inclusion of digestible carbohydrate may well be variable depending upon the overall balance of protein, fat, and carbohydrate as well as the total energy content of the salmonid diet.

Both liver glycogen content (LG) and liver:body weight ratio (LB) increased with increasing dietary glucose but leveled off above 10−15% glucose (Table 4). The amount of LG and magnitude of LB in relation to the amount of dietary glucose were less than that observed by Hilton and Atkinson (1982). Recent unpublished observations in our laboratory have indicated that in rainbow trout reared on low lipid, 40% crude protein diets, there is generally a linear relationship between LG, LB, and digestible carbohydrate level.

Hilton and Atkinson (1982) suggested that trout fed high carbohydrate, low lipid diets had increased activity of liver fructose-1,6-diphosphatase (FD) and G6PD for recycling of triosephosphates and generation of reducing equivalents for

TABLE 4. The liver:body weight ratio (mean of 60 samples per treatment ± standard deviation) and liver glycogen (mean of 12 samples per treatment ± standard deviation) content of trout after 12 wk on the test diets.

Parameter	Temp. °C	Diet number 1	2	3	4	5	6
Liver:body weight ratio (× 100)	15	1.2±0.1	1.3±0.2	1.4±0.2	1.6±0.3	1.6±0.3	1.8±0.3
	11	1.2±0.3	1.4±0.4	1.6±0.3	1.7±0.3	1.9±0.3	1.8±0.5
Liver glycogen (%)	15	4.3±0.7	5.1±0.8	5.9±0.8	5.9±1.1	7.3±1.8	8.4±1.8
	11	4.2±0.7	5.6±0.9	8.7±0.9	11.2±1.7	9.3±1.9	10.5±1.9

TABLE 5. The plasma glucose and protein levels of trout after 12 wk on the test diets. (Results based upon the mean of eight samples per treatment ± standard deviation.)

Parameter	Temp. °C	Diet number 1	2	3	4	5	6
Plasma glucose (mg/dL)	15	60.6±6.1	59.9±5.9	73.9±9.5	63.4±7.7	70.4±10.1	62.8±8.8
	11	57.5±6.5	53.2±7.2	66.3±5.5	76.5±8.8	76.2±10.2	72.7±10.2
Plasma protein (mg/mL)	15	46.5±5.1	44.9±5.9	44.5±6.0	46.1±4.8	46.5±4.8	49.6±5.2
	11	46.6±5.0	52.3±6.1	49.0±5.3	49.7±5.2	46.5±4.8	40.7±9.2

TABLE 6. Liver glucose-6-phosphate dehydrogenase and pyruvate kinase activity of trout after 12 wk on the test diets. (Results are the mean of four to six fish per treatment ± standard deviation; values with the same superscript are not significantly different.)

Parameter	Temp. °C	Diet number 1	2	3	4	5	6
Glucose-6-phosphate dehydrogenase	15	3.9 ± 1.4^{a}	5.0 ± 1.3^{ab}	6.7 ± 1.6^{ab}	9.9 ± 4.5^{abc}	11.4 ± 4.1^{bc}	13.8 ± 5.9^{c}
	11	6.0 ± 1.1^{a}	8.3 ± 7.2^{a}	8.4 ± 2.9^{a}	12.0 ± 4.4^{ab}	16.5 ± 2.6^{b}	11.3 ± 3.2^{ab}
Pyruvate kinase	15	4.2±1.8	5.6±1.4	7.4±5.1	10.0±5.5	9.5±5.9	12.6±4.8
	11	9.7±3.9	9.7±3.9	12.0±6.5	15.7±5.5	13.9±4.8	13.5±3.1

fat synthesis. In the present study, liver G6PD activity also increased with increased glucose levels (Table 6); however, no further stimulation of enzyme activity occurred above 20% glucose at 11°C and maximal activity was reduced in comparison to the former study (13.5 vs. 10.1 μmol of substrate utilized·min^{-1}·100 g BWT^{-1} at 15°C). This may indicate that there was a less marked increase in hexose monophosphate shunt (HMS) activity required for generation of reducing equivalents for fat synthesis. The present test diets contained an optimal level of lipid, thus reducing the necessity for fat synthesis. Carcass lipid levels were observed to be essentially the same in all groups (Table 3).

Although care must be taken when extrapolating from in vitro enzyme activity measurements to in vivo conditions, it is interesting to note that liver glycogen also increased with increasing dietary glucose but then plateaued above 20% glucose. Hilton and Atkinson (1982) suggested that recycling of triosephosphates with subsequent buildup of glucose-6-phosphate could contribute to excess glycogen deposition in the livers of trout reared on diets with high levels of digestible carbohydrate. The plateauing of LG and LB in this study would then be consistent with the reduced increase in activity of liver G6PD.

When considered on the basis of G6PD and PK responses to the increase in dietary glucose, the maximum tolerable level of glucose would seem to be below the 25% fed in diet 6. It remains to be explained why this apparent limit in metabolic adaptation is not necessarily translated into impaired growth efficiency in the fish. In this respect it should be noted that α-cellulose was used as a non-nutritive filler in the test diets (Table 1). Recent research has shown that excess fiber, i.e. greater than 10%, can reduce the growth of rainbow trout (Hilton et al. unpublished observations). Therefore, it is possible that the increased levels of dietary fiber, particularly in the diets low in glucose, could be masking the true growth response of the trout. Further studies are required to elucidate more fully these observations.

The fate of the excess glucose that is digested by the trout remains to be explained if it is not efficiently utilized as an energy source or for fatty acid synthesis. This cannot be readily discerned in the present study and further work is required to determine the metabolic fate of the excess glucose.

The apparent digestion coefficients of glucose in the different groups of trout were uniformly high (96−99%) and were not significantly affected by either water temperature or level of dietary glucose inclusion (up to 25%). In fish, carbohydrate digestibility generally decreases as the dietary level increases (NRC 1977). Similarly, water temperature may affect the

digestibility of certain nutrients in fish (NRC 1977), but this was not apparent in the case of glucose. Greater extremes of temperature and glucose inclusion levels than used in this study may have produced a different response in the trout.

It was also noted that trout reared at 11°C with the same dietary glucose level tended to have higher LG and LB than trout reared at 15°C (Table 4). It is known that colder water temperatures result in excess storage of glycogen in salmonid livers (NRC 1973). Hochachka and Hayes (1962) suggested that there is an increased utilization of HMS in cold acclimated fish, associated with the increased requirement for reducing equivalents as NADPH needed to permit a shift towards enhanced fatty acid synthesis at low temperatures. The higher liver G6PD and PK activities (assayed at 15°C) observed in the fish reared at 11°C at all but the highest levels of dietary glucose lend credence to this view. It is possible that the increased utilization of HMS in trout reared at 11°C as compared with 15°C may account for the increased LG and LB of fish in this study. Increased utilization of HMS and possibly increased recycling of triosephosphates would increase the liver concentration of glucose-6-phosphate in trout at 11°C thus increasing liver glycogen synthesis. Further elucidation of these hypotheses is being carried out in our laboratory.

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ARTHUR, D. 1970. The determination of chromium in animal feed and excreta by atomic absorption spectrophotometry. Can. Spectrosc. 15: 1–4.

BERGOT, F. 1979. Carbohydrate in rainbow trout diets: effect of level and source of carbohydrate and number of meals on growth and body composition. Aquaculture 18: 157–168.

BLIGH, E. G., AND W. G. DYER. 1959. A rapid method of total lipid extraction and purification. Can. J. Biochem. Physiol. 37: 911–917.

BUHLER, D. R., AND J. E. HALVER. 1961. Nutrition of salmonid fishes: IX Carbohydrate requirement of chinook salmon. J. Nutr. 74: 307–318.

CHO, C. Y., S. J. SLINGER, AND H. S. BAYLEY. 1976. Influence of level and type of dietary protein, and of feeding level on feed utilization by rainbow trout. J. Nutr. 106: 1547–1556.

FREEDLAND, R. A. 1967. Effect of progressive starvation on rat liver enzyme activities. J. Nutr. 91: 489–495.

HILTON, J. W., AND J. L. ATKINSON. 1982. Response of rainbow trout to increased levels of available carbohydrate in practical trout diets. Br. J. Nutr. (In press)

HILTON, J. W., AND S. J. SLINGER. 1981. The nutrition and feeding of rainbow trout. Can. Spec. Pub. Fish. Aquat. Sci. 55: 15 p.

HOCHACHKA, P. W., AND F. R. HAYES. 1962. The effect of temperature acclimation on pathways of glucose metabolism in trout. Can. J. Zool. 49: 261–270.

HORWITZ, W., P. CHICHILO, AND H. REYNOLDS. [ed.] 1970. AOAC Methods, Official methods of analysis of the official analytical chemists. 11th ed. Association of Official Analytical Chemists, Washington, DC. 1015 p.

LOWRY, O. H., N. J. ROSEBROUGH, A. L. FARR, AND D. J. RANDALL. 1951. Protein measurement with the Folin phenol reagent. J. Biol. Chem. 193: 265–275.

LUQUET, P. 1971. Efficacité des protéines en relation avec leur taux d'incorporation dans l'alimentation de la truite arc-en-ciel. Ann. Hydrobiol. 2: 175–186.

MURAT, J. C., AND A. SERAFTY. 1974. Simple enzymatic determination of polysaccharide (glycogen) content of animal tissues. Clin. Chem. 20: 1576–1577.

NATIONAL RESEARCH COUNCIL. 1973. Nutrient requirements of trout salmon and catfish. Nutrient requirements of domestic animals No. 11. Natl. Acad. Sci. Washington, DC. 57 p.

1977. Nutrient requirements of warm water fishes. Nutrient requirements of domestic animals. Nat. Acad. Sci. Washington, DC. 78 p.

PHILLIPS, A. M., A. V. TUNISON, AND D. R. BROCKWAY. 1948. The utilization of carbohydrates by trout. Fish. Res. Bull. 11.

POGSON, C. I. 1968. Two interconvertible forms of pyruvate kinase in adipose tissue. Biochem. Biophys. Res. Commun. 30: 297–302.

REINITZ, G. L., L. E. ORME, C. A. LEMM, AND F. N. HITZEL. 1978. Influence of varying lipid concentrations with two protein concentrations in diets for rainbow trout (*Salmo gairdneri*) Trans. Am. Fish. Soc. 107: 751–754.

STEELE, R. G. D., AND J. H. TORRIE. 1960. Principles and procedures of statistics. McGraw-Hill, New York, NY. 481 p.

TAKEUCHI, T., T. WATANABE, AND C. OGINO. 1978. Optimum ratio of protein to lipid in diets of rainbow trout. Bull. Jpn. Soc. Sci. Fish. 44(6): 683–688.

1979. Availability of carbohydrate and lipid as dietary energy sources for carp. Bull. Jpn. Soc. Sci. Fish. 45(8): 977–982.

Ecological Responses of Hydropsychid Caddisflies to Stream Regulation

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Based on the river continuum theory and preliminary investigation in the upper Flathead River (British Columbia and Montana), we expected a sequential change in the hydropsychid fauna from large Arctopsychinae species in low-order streams to smaller Hydropsychinae in the higher-order rivers. *Parapsyche elsis* was found in small 1st- and 2nd-order streams and was replaced by *Arctopsyche grandis* as the dominant net-spinning caddisfly in 3rd- and 4th-order creeks. Three Hydropsychinae species first appeared in 4th-order creeks and became dominant in the 5th-order river, although *A. grandis* was still present. Site-specific degree-days (annual) increased progressively down the longitudinal gradient from 1200 degree-days in low-order, high-mountain streams to 2400 degree-days in the 5th-order river. However, hypolimnion tail waters from the regulated South Fork altered the thermal regime in the 6th-order mainstream from an expected 2600 annual degree-days to 2050 degree-days. The diurnally fluctuating discharge pattern from the hydroelectric dam also resulted in sloughing of attached algae into the river seston. The decrease in annual degree-days and increase in sestonic particulate organic matter produced conditions similar to those in 4th-order creeks. Hydropsychids responded to the effects of stream regulation by reflecting population structure found in lower-order creek reaches. *Arctopsyche grandis* was the dominant collector-filter feeder in the regulated mainstream river segment and Hydropsychinae abundance was significantly lower than in unregulated, 5th-order river segments. We interpret the alteration of environmental parameters and corresponding faunal response as a reset of the river continuum caused by stream regulation.

Key words: Hydropsychidae, Trichoptera, river, ecosystem, stream regulation, Flathead River, stream continuum, zoobenthos, temperature, particulate organic matter

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En se fondant sur la théorie du continuum des rivières et une investigation préliminaire dans le haut de la rivière Flathead (Colombie-Britannique et Montana), on s'attendait à un changement graduel de la faune hydropsychide, depuis les grandes espèces d'Arctopsychinae dans les cours d'eau d'ordre inférieur aux Hydropsychinae plus petits dans les rivières d'ordre supérieur. *Parapsyche elsis* se trouve dans les petits cours d'eau de 1er et 2^{e} ordre, et est remplacé par *Arctopsyche grandis* comme la phrygane fileuse de filets-pièges dominante dans les ruisseaux de 3^{e} et 4^{e} ordre. Trois espèces d'Hydropsychinae apparaissent d'abord dans les ruisseaux de 4^{e} ordre et deviennent dominantes dans les rivières de 5^{e} ordre, bien que *A. grandis* y soit encore présent. Les jours-degrés (annuels) particuliers au site augmentent progressivement en descendant le gradient longitudinal, de 1 200 dans les cours d'eau d'ordre inférieur des hautes montagnes à 2 400 dans la rivière de 5^{e} ordre. Cependant, le régime thermique dans le cours d'eau principal de 6^{e} ordre est modifié par les eaux d'aval de la rivière South Fork à débit contrôlé : il passe d'un nombre anticipé de jours-degrées de 2 600 à 2 050. Les fluctuations diurnes de l'effluent du barrage hydro-électrique font également que les algues fixées se détachent et passent dans le seston de la rivière. La diminution du nombre de jours-degrés annuels et l'augmentation de la matière particulaire sestonique produisent des conditions semblables à celles des ruisseaux de 4^{e} ordre. Les hydropsychides réagissent aux effets de la régulation des cours d'eau par une structure de population rencontrée dans des portions de ruisseaux d'ordre inférieur. *Arctopsyche grandis* est l'organisme dominant collecteur ou se nourrissant par filtration dans le segment principal contrôlé de la rivière, et

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l'abondance des Hydropsychinae est nettement inférieure à celle des segments non contrôlés de rivière de 5^{e} ordre. Nous interprétons la modification des paramètres ambiants et la réaction faunique correspondante comme un réajustement du continuum fluvial causé par la régulation des cours d'eau.

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A dynamic gradient of macroinvertebrate species composition exists longitudinally along streams and rivers. Small headwater streams of deciduous forest biomes are dominated by their terrestrial setting, depending largely upon the input of coarse particulate organic matter from allochthonous sources (Cummins 1973). Headwater streams are characterized by extensive forest overstory and riparian vegetation, which limits incident light to the stream. Periphyton production is reduced and diurnal temperature flucutation dampened. Medium-sized rivers often have less canopy permitting higher levels of autotrophy, greater diurnal and seasonal temperature fluctuation, and less dependence on terrestrial organic input (Vannote et al. 1980). Macroinvertebrate trophic groups have been shown to reflect the variation in availability and derivation of energy sources (Cummins 1973; Wallace et al. 1977; Anderson and Sedell 1979). Western montane streams and rivers may be less dependent on autumnal allochthonous detrital sources than lotic environments of the deciduous forest biome; autotrophy may be a significant contributing factor to the energy budget (Minshall 1978). The different food sources of coniferous forest litter (Sedell et al. 1975) and the greater autotrophy, in addition to other environmental factors such as temperature, substrate, and gradient, establish the basis for a typical montane zoobenthic fauna, which sequence in a finite distribution along stream and river gradients (Wiggins and Mackay 1978). However, virtually no river system in North America remains unregulated by dams or diversions (Stanford and Ward 1979). The mechanisms by which regulation impacts distributions of lotic zoobenthos is not well understood (Ward and Stanford 1979).

Net-spinning caddisfly larvae (Hydropsychidae) occupying lotic environments often comprise a significant portion of zoobenthic biomass (Cushing 1963; Ward and Short 1978) by utilization of particulate organic matter in stream seston (Cummins 1973; Wallace 1975; Gordon and Wallace 1975; Hauer and Stanford 1981). Capture net mesh size, surface area, and position in the current are important factors used by filter-feeding trichopterans to partition particulate organic matter in stream seston (Edington 1968; Wallace et al. 1977). Hatching, growth, emergence, and adult activity may largely be a function of thermal cues and/or a summation of temperature units (i.e. degree-days) (sensu Andrewartha and Birch 1954); Gose (1970) used temperature dynamics to explain the life history sequence of a Japanese hydropsychid, *Stenopsyche griseipennis*.

While conducting ecosystem level studies of the Flathead River system (Montana–British Columbia), we observed similarities in species composition of net-spinning caddisfly communities residing in a 6th-order (Strahler 1957) segment receiving cold, hypolimnial discharges from an upstream reservoir, and lower-order segments. *Parapsyche elsis* dominated the net-spinning collector functional group in 1st- and 2nd-order streams. *Arctopsyche grandis* replaced *P. elsis* as the dominant hydropsychid in 3rd- and 4th-order creeks. *Hydropsyche cockerelli*, *H. oslari*, and *H. occidentalis* were the most abundant net-spinning caddisflies in the 5th-order tributary rivers above the confluence of the regulated South Fork. Below the confluence of the regulated South Fork, *A. grandis* was again the dominant hydropsychid. We hypothesized that the disjunct distribution of Hydropsychidae in the Flathead River represented a predictable response to the "reset" thermal and particulate organic matter (POM) regima caused by regulated hypolimnial discharges. We measured the response in terms of distributions and abundance at different locations along the stream continuum.

Study Area

The Flathead River originates in heavily glaciated basins along the Continental Divide in northwestern Montana and southeastern British Columbia. First- to 4th-order tributaries derived from springbrooks or snowfields feed the three main forks of the river (Fig. 1). The streams are cold, rhithron-type habitats, although alluvial deposits are extensive on the riverine (4th to 6th order) flood plains and create large areas of hyporheic habitat (Stanford and Gaufin 1974). The rivers are erosive during spring runoff, when discharge may increase from 10 to 100 times mean flow (260 $m^3 \cdot s^{-1}$ in mainstream). The waters carry moderate dissolved solids, except in some poorly buffered streams draining clastic bedrocks in Glacier National Park. Headwater streams originate from snowfields in tundra areas (above 2300 m) and in springs within coniferous forest. Second- and 3rd-order streams are predominately canopied by forest overstory of Douglas fir and western larch, while the riverine segments are exposed to the sun. Physics, chemistry, and morphology of the system are detailed elsewhere (Stanford et al. 1982).

About 6 km above the confluence with the combined waters of the North and Middle Forks, the South Fork is impounded by a 153-m-high Hungry Horse Dam creating a 55-km-long Hungry Horse Reservoir (Fig. 1). The river below the dam has been significantly altered as a result of hypolimnial discharges; flow may fluctuate between 7.5 $m^3 \cdot s^{-1}$ and 300 $m^3 \cdot s^{-1}$ diurnally. The substrate has become heavily armored similar to other regulated rivers (Simons 1979). Hypolimnial discharges have resulted in an isothermal (5°C ± 2) temperature regime. Substantial growths of *Gomphonema geminatum* and *Ulothrix zonata* cover the surface of the substrate in response to lack of scour during spring runoff and the comparatively higher dissolved nutrient levels in hypolimnion waters (Stanford et al. 1982). The effects of stream regulation are somewhat ameliorated in the mainstream by natural flows from the North and Middle Forks. However, flow fluctuations, as a result of power generation at the dam on the South Fork, profoundly vary the wetted perimeter in the meandering mainstream channel.

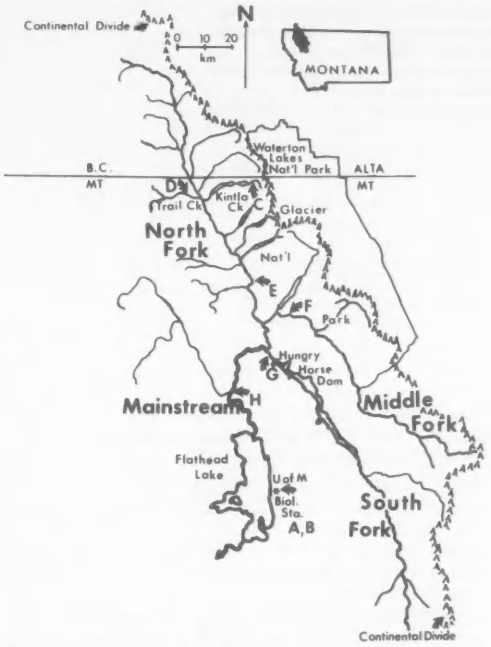

FIG. 1. The Flathead River Basin, Montana, and location of sampling sites.

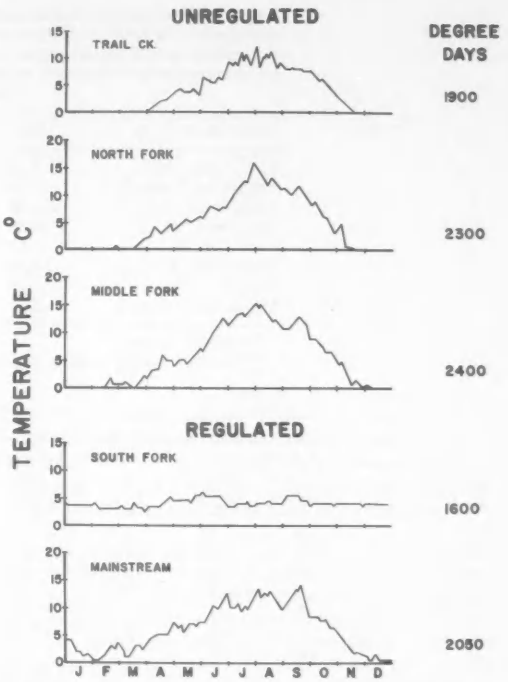

FIG. 2. Thermal regima and temperature summations measured in 1979 at selected creek and riverine sites on the Flathead River continuum.

Periphyton is more profuse in the mainstream (also *Ulothrix* and *Gomphonema*) compared to unregulated segments, but is scoured during spring runoff.

Methods

Quantitative, time–series data were collected at eight locations (Fig. 1). Stations A (1st order, springbrook) and B (2nd order) were located on protected reaches of small streams on the University of Montana Biological Station grounds. Stations C (3rd order) and D (4th order) were located on reaches of North Fork tributaries not influenced by lakes. Riverine sites were established on the unregulated North (station E, 5th order) and Middle (station F, 5th order) Forks about 20 km upstream from their confluence. Two stations were located on segments regulated by Hungry Horse Dam: station G (5th order, regulated) on the South Fork about 5 km from the dam, and station H on the mainstream about 15 km downstream from the South Fork confluence.

Hydropsychids were collected over a 5-yr period, 1977–81. Larvae were quantified by collecting replicated samples (usually five) using a modified "kick net" procedure. Specimens were dislodged by hand and foot action within a 0.5-m^2 area over a 1-min sampling interval and retained in a large, cod-ended net held downstream. Variance estimates from replicate samples obtained with this procedure were comparable to other techniques (e.g. colonization samplers) and permitted collection of large areas of the river bottom (see Stanford et al. 1982). For the riverine sites, a large number of quantitative samples were obtained to cover all substrate types. Immatures were collected monthly, although high water prevented quantitative sampling during spring runoff in late April, May, and June. Adults were collected by sweeping shoreline vegetation and by attraction to UV lights.

Continuous recording thermographs were maintained (1977–81) by the United States Geological Survey on the North Fork and by Montana Department of Fish, Wildlife, and Parks on the Middle Fork, the mainstream river below the South Fork confluence and Trail Creek. Data from these recorders and our own recorders in Roy's and Yellow Bay creeks were used to determine accumulated heat units (i.e. degree-days, see Baskerville and Emin 1968). In all cases, the temperature probes were maintained in or near the thalweg to ensure accurate records (see Stanford et al. 1982).

Particulate organic matter (POM) concentrations in seston were measured in time–series at each site during portions of the study period (1977–81) (see Stanford et al. 1982). POM values were determined by CO_2 liberation procedure (Menzel and Vaccaro 1964) on an Oceanography International 0524B total carbon system.

Our taxonomic identifications were verified by Dr G. B. Wiggins. He recommended we retain use of the genus name *Hydropsyche*, as opposed to *Symphitopsyche* (see Ross and

TABLE 1. Concentrations of particulate organic matter ($mgC \cdot L^{-1}$) in seston at eight locations in the Flathead River Basin, Montana, during low flow months (i.e. excluding spring runoff period, April–July) 1977–81.

Station name	Particulate organic matter			Sample size[b]
	Mean	SD	Range	
Roy's Creek, A	0.11	0.07	0.05–0.24	5
Yellow Bay Creek, B	0.18	0.08	0.04–0.25	5
Kintla Creek, C	0.04	0.02	0.02–0.08	6
Trail Creek, D	0.09	0.03	0.06–0.14	10
North Fork, E	0.11	0.06	0.03–0.27	20
Middle Fork, F	0.09	0.06	0.03–0.24	21
South Fork, G[a]	0.07	0.05	0.02–0.22	33
Mainstream, H[a]	0.12	0.08	0.05–0.41	28

[a]Regulated segment.
[b]Number of monthly samples (see text).

TABLE 2. Estimated density $\cdot m^{-2}$ ($\bar{x} \pm$ SD) of Hydropsychidae at eight locations longitudinally distributed along the Flathead River, Montana, from headwaters to mainstream.

Station	Stream order	*P. elsis*	*A. grandis*	*H. cockerelli*	*H. oslari*	*H. occidentalis*
A	1	0	0	0	0	0
B	2	1	0	0	0	0
C	3	7±5	[b]	0	0	0
D	4	7±6	3±2	[b]	[b]	0
E	5	0	22±14	100±44	79±34	4±4
F	5	0	35±29	338±144	323±146	17±24
G[a]	5	0	0	0	0	0
H[a]	6	0	268±177	13±9	4±8	4±4

[a]Regulated segment.
[b]Species known to be present, but not collected in quantitative samples.

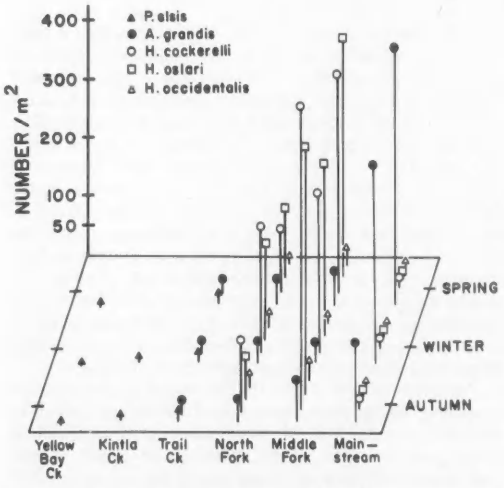

FIG. 3. Relative seasonal abundance (no. m^{-2}) of larvae of *Arctopsyche grandis*, *Hydropsyche cockerelli*, *H. oslari*, and *H. occidentalis* at six creek and river sites on the Flathead River continuum.

Unzicker 1977; Schmid 1979), until questions involving taxonomy of the Bifida group are resolved.

Results and Discussion

TEMPERATURE

Plots of daily temperatures from the various sampling sites revealed an expected increase in summer temperatures down the longitudinal gradient of the river basin (Fig. 2). However, mainstream river temperatures during summer and early fall were significantly decreased as a result of cold hypolimnion discharge from Hungry Horse Reservoir. The number of degree-days in the mainstream river approached that found in Trail Creek, while temperatures over the annual cycle in the South Fork tailwaters were similar to the more constant conditions observed in Roy's ($\bar{x}$ = 7°C ± 2°C; 2550 degree-days) and Yellow Bay ($\bar{x}$ = 7°C ± 4°C, 2750 degree-days) creeks, which are fed by groundwaters.

PARTICULATE ORGANIC MATTER

The headwater streams (1st–3rd order) in the Flathead River basin generally contain greater amounts of organic matter within the benthos than do the higher-order reaches; also, the percentage of material less than 150 μm in size

TABLE 3. Interval analysis of seasonal mean abundance of Hydropsychidae species present in the North Fork (site E, unregulated), the Middle Fork (site F, unregulated), and the mainstream Flathead River (site H, regulated). (nsd, no significant difference, *significantly different ($P < 0.05$), **highly significantly different ($P < 0.01$).)

	Site contrasts	*A. grandis*	*H. cockerelli*	*H. oslari*	*H. occidentalis*
Fall	E vs. F	nsd	E<F*	E<F**	nsd
	E vs. H	E<H*	E>H*	E>H**	nsd
	F vs. H	F<H*	F>H*	F>H**	nsd
Winter	E vs. F	nsd	nsd	E<F*	nsd
	E vs. H	E<H**	E>H*	E>H**	nsd
	F vs. H	F<H**	F>H*	F>H**	nsd
Spring	E vs. F	nsd	nsd	E<F**	nsd
	E vs. H	E<H**	E>H*	E>H**	nsd
	F vs. H	F<H**	F>H*	F>H**	nsd

increases downstream (Stanford et al.1982). Sites A and B were heavily laden with allochthonous material such as leaves, needles, sticks, and tree trunks. These materials were replaced by processed, fine particulates and autochthonous materials at the riverine sites. Sestonic POM concentrations were closely associated with discharge at all sites; the highest values were recorded during spring runoff in May–June each year. Analyses of data from low flow months (i.e. August–March) indicated presence of coarser POM drifting at the upstream sites, while generally low concentrations of finer materials were present in seston at sites C, D, E, and F (3rd–5th order, unregulated). Concentrations of POM in seston were also low in the dam tailwaters at site G (Table 1), in spite of greatly fluctuating flows and the presence of profuse periphytic algae in the minimum flow portion of the channel. However, Stanford et al. (1982) demonstrated concentrations of POM in seston increased as a function of distance from the dam. Downstream at site H (6th order, regulated), greater amounts of POM were present in seston over time (Table 1), mostly due to periphyton sloughed by the regulated discharges during late summer, fall, and winter.

Hydropsychid nets in the mainstream were frequently observed heavily packed with *Ulothrix* and other algae filtered from seston. These algae were a significant component of *A. grandis* diet in the river segment (Hauer and Stanford 1981).

DISTRIBUTION AND ABUNDANCE

Hydropsychid caddisflies were not present in the headwater springbrook, Roy's Creek (site A, 1st order). Large, semivoltine *P. elsis* were the only net-spinning caddisflies inhabiting site B (2nd order), Yellow Bay Creek; these larvae were not abundant, averaging <5 individuals·m^{-1} (Table 2; Fig. 3). *Parapsyche elsis* and similarly sized *A. grandis* were found together in Trail Creek (site D, 4th order). At the 3rd-order site, Kintla Creek, *A. grandis* was collected, but not in quantitative samples. In general, it appeared that *P. elsis* was comparatively more stenothermic than *A. grandis*. Kintla Creek was about 600 degree-days colder than Trail Creek in 1980–81, the only period of temperature record, and *A. grandis* may be near the limit of its upstream distribution at Kintla Creek site. As the two species build nets of similar mesh size (4–6 μm), interspecific competition for food and retreat locality may also be important in the observed distribution pattern.

In the riverine segments (i.e. sites E, F, G, and H; 5th–6th order), the distribution data were more complicated and involved *A. grandis* and the three Hydropsychinae species; *P. elsis* was never collected at sites below 4th order (Fig. 3). *Arctopsyche grandis*, *H. cockerelli*, *H. oslari*, and *H. occidentalis* were found in the North Fork (site E), Middle Fork (site F), and the mainstream (site G), but population densities varied between sites (Table 2). While the smaller Hydropsychinae dominated the net-spinning component of the zoobenthos in the North and Middle Forks, *A. grandis* was exceptionally abundant in the mainstream. No hydropsychids were present in the cold tailwaters of the South Fork from Hungry Horse Dam to the mainstream confluence (see Table 2, site G).

Interval analysis for comparison of samples of unequal replication and variance (Scheffe' 1959) verified that *A. grandis* was significantly more abundant in the mainstream in comparison to the North and Middle Forks. Conversely, *H. cockerelli* and *H. oslari* dominated the net-spinning component of the macroinvertebrate community of the Middle Fork (Table 3). Species dominance among the Hydropsychidae in the North Fork was indistinct (Fig. 3); however, *H. cockerelli* and *H. oslari* appeared to be most abundant (Table 3).

Specific life histories may play a role in the observed distribution patterns. *Arctopsyche grandis* (Hauer and Stanford 1981) and probably *P. elsis* completed the life cycle in 2 yr, while the Hydropsychinae species were univoltine with species-specific patterns of growth and emergence (Hauer and Stanford unpublished data). The exact nature of mechanisms defining habitat (e.g. stream order) preference will not be clear until these species are successfully reared in experimental temperature and food gradients. However, the differential segregation of these species along the stream continuum in the Flathead River appeared to be closely correlated to attendant segregation of temperature patterns and POM con-

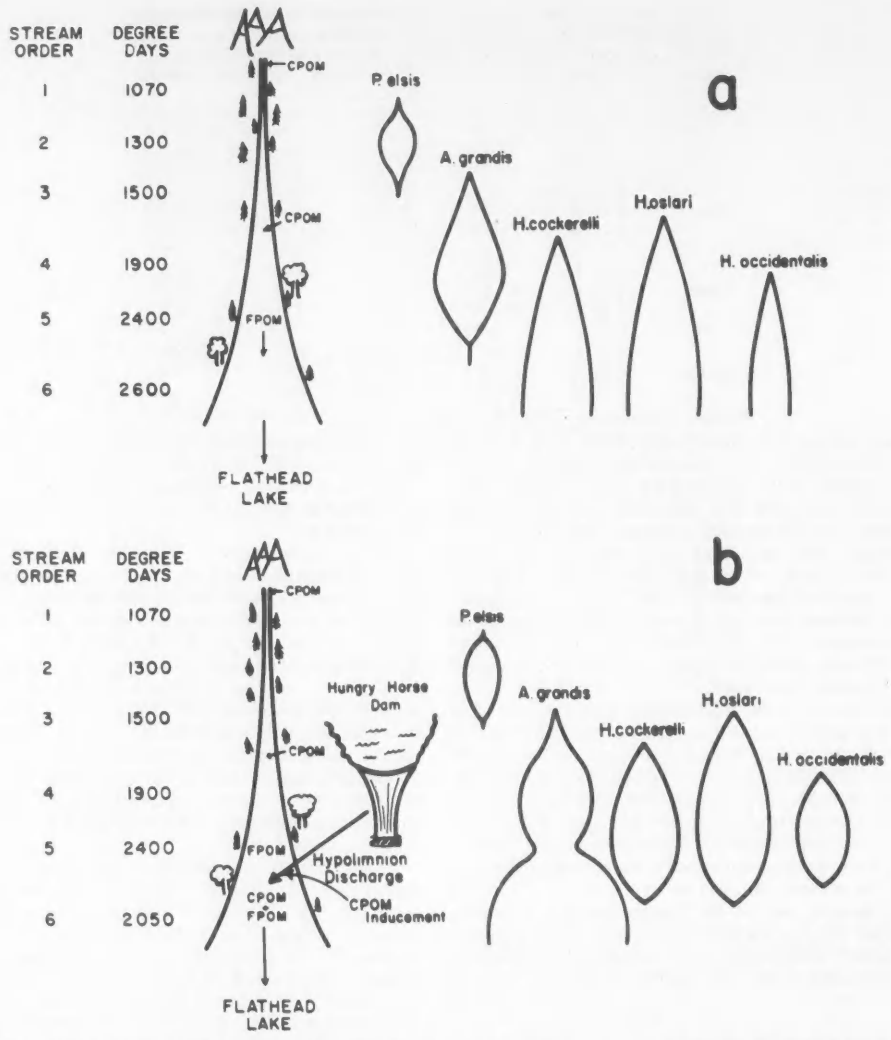

FIG. 4. Distribution of selected parameters and the Hydropsychidae down the river continuum of the Flathead River basin: (a) hypothetical distribution without Hungry Horse Dam on the South Fork; (b) as it exists with Hungry Horse Dam on the South Fork.

centrations among stream orders.

The observed patterns of *A. grandis* and Hydropsychinae distribution and abundance in the mainstream river was an apparent manifestation of river regulation. Cold-water discharge and diurnal variability of discharge from Hungry Horse Reservoir resulted in suppression of the mainstream thermal maxima and alteration of seston dynamics. Additional evidence in support of this conclusion was reflected in the dam tailwaters on the South Fork, where no net-spinning caddisflies were collected. Physicochemistry of the tailwaters was very similar to 1st-order springbrooks in the drainage (e.g. constant annual and diurnal thermal regime), which also were not inhabited by the Hydropsychidae. The lack of thermal cues in these non-fluctuating environments may be particularly important in explaining failure of Hydropsychidae to inhabit them (Ward and Stanford 1982a).

STREAM CONTINUUM AND STREAM REGULATION

Prior to the construction of Hungry Horse Dam, comparatively warmer waters and availability of sestonic FPOM probably favored the smaller Hydropsychinae species over

A. grandis in the mainstream river (Site H) above Flathead Lake. Placed in the context of a continuum, the hydropsychid community in headwater streams is dominated by *P. elsis*, grades to domination by *A. grandis* in 4th- and upper 5th-order reaches, and probably culminated with the Hydropsychinae dominating in the 6th-order mainstream (Fig. 4a). This interpretation is consistent with other studies demonstrating downstream dominance of the smaller hydropsychid species (Wallace et al. 1977; Wiggins and Mackay 1978; Alstad 1980). However, cold-water discharges from Hungry Horse Dam, coupled with increased concentrations of CPOM, actually exert a "reset" influence on the Flathead River continuum by eliminating net-spinning caddisflies from the South Fork below the dam and significantly favoring *A. grandis* over the Hydropsychinae species in the mainstream (Fig. 4b).

The river continuum concept (Vannote et al. 1980) predicts a reset of physicochemical and biotic parameters of larger-order rivers in response to confluence of lower-order tributaries. Continuum reset in the natural stream has been attributed primarily to type and size of organic matter introduced by smaller tributary streams and to a lesser extent, decrease in temperature. Unlike natural reset mechanisms, in which effects of the reset continue for comparatively short distances downstream (generally a few hundred metres), the reset created by stream regulation frequently involves significant thermal as well as trophic modifications and continues for several kilometres (Ward and Stanford 1979). The degree to which a reset manifests is dependent upon which parameters are affected, the degree to which these parameters are changed from the annual regime, and the temporal sequencing of these changes.

Resetting of the river continuum, as a result of stream regulation, is probably a universal occurrence and is especially pronounced in rivers receiving hypolimnial discharges. Downstream displacement of species dominating upstream communities into areas influenced by stream regulation may be expected where habitat, thermal regima, and the energy base (e.g. size and quality of POM) simulate upstream areas. This interpretation supports the serial discontinuity concept of lotic ecosystems (Ward and Stanford 1982b), which suggests stream regulation via hypolimnial release may manifest a downstream shift in the area of maximum environmental heterogeneity and attendant biotic maxima. However, important mechanisms (e.g. nutrient spiralling, sensu Newbold et al. 1981; agglutination of POM, sensu Kitchell et al. 1979; insect immigration and emigration, sensu Müller 1974; and maintenance of genetic integrity in populations, sensu Levins 1968), which dimension "resets" in regulated stream ecosystems, remain to be fully elucidated and quantified in different environmental and geographic settings.

Acknowledgments

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ALSTAD, D. N. 1980. Comparative biology of the common Utah Hydropsychidae (Trichoptera). Am. Midl. Nat. 103: 167–174.

ANDERSON, N. H., AND J. R. SEDELL. 1979. Detritus processing by macroinvertebrates in stream ecosystems. Annu. Rev. Entomol. 24: 351–377.

ANDREWARTHA, H. G., AND L. C. BIRCH. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, IL. 782 p.

BASKERVILLE, G. L., AND P. EMIN. 1968. Rapid estimation of heat accumulation from maximum and minimum temperatures. Ecology 50: 514–517.

CUMMINS, K. W. 1973. Trophic relations of aquatic insects. Annu. Rev. Entomol. 18: 183–206.

CUSHING, C. E. 1963. Filter-feeding insect distribution and planktonic food in the Montreal River. Trans. Am. Fish. Soc. 92: 216–219.

EDINGTON, J. M. 1968. Habitat preference in net-spinning caddis larvae with special reference to the influence of running water. Ecology 37: 675–692.

GORDON, A. E., AND J. B. WALLACE. 1975. Distribution of the family Hydropsychidae (Trichoptera) in the Savannah River basin of North Carolina, South Carolina and Georgia. Hydrobiology 46: 405–423.

GOSE, K. 1970. Life history and instar analysis of *Stenopsyche griseipennis* (Trichoptera). Jpn. J. Limnol. 81: 96–107.

HAUER, F. R., AND J. A. STANFORD. 1981. Larval specialization and phenotypic variation in *Arctopsyche grandis* (Trichoptera: Hydropsychidae). Ecology 62: 645–653.

KITCHELL, J. F., R. V. O'NEILL, D. WEBB, G. W. GALLEPP, S. M. BARTELL, J. F. KOONCE, AND B. S. AUSMUS. 1979. Consumer regulation of nutrient cycling. BioScience 29: 28–34.

LEVINS, R. 1968. Evolution in changing environments. Princeton Univ. Press, Princeton, NJ. 120 p.

MENZEL, D. W., AND F. R. VACCARO. 1964. The measurements of dissolved and particulate carbon in sea water. Limnol. Oceanogr. 9: 138–142.

MINSHALL, G. W. 1978. Autotrophy in stream ecosystems. BioScience 28: 767–771.

MÜLLER, K. 1974. Stream drift as a chronobiological phenomenon in running water ecosystems. Annu. Rev. Ecol. Syst. 5: 309–323.

NEWBOLD, J. D., J. W. ELWOOD, R. V. O'NEILL, AND W. VAN-WINKLE. 1981. Measuring nutrient spiralling in streams. Can. J. Fish. Aquat. Sci. 38: 860–863.

ROSS, H. H., AND J. D. UNZICKER. 1977. The relationship of the genera of American Hydropsychinae as indicated by phallic structures (Trichoptera, Hydropsychidae). J. Georgia Ent. Soc. 12: 298–312.

SCHEFFE', H. 1959. The analysis of variance. John Wiley & Sons, Inc., New York, NY. 477 p.

SCHMID, F. 1979. On some new trends in Trichopterology. Entomol. Soc. Can. Bull. 11: 48–57.

SEDELL, J. R., F. J. TRISKA, AND N. S. TRISKA. 1975. The processing of conifer and hardwood leaves in two coniferous forest streams. I. Weight loss and associated invertebrates. Verh. Int. Verein. Limnol. 19: 1617–1627.

SIMONS, D. B. 1979. Effects of stream regulation on channel morphology, p. 95–111. *In* J. V. Ward and J. A. Stanford [ed.] The ecology of regulated streams. Plenum Press, New York, NY. 398 p.

STANFORD, J. A., AND A. R. GAUFIN. 1974. Hyporheic communities of two Montana rivers. Science 185: 700–702.

STANFORD, J. A., F. R. HAUER, J. D. COULTER, T. J. STUART, R. L. HENRY, B. K. ELLIS, AND S. BERTÉ. 1982. Biophysical studies of the Flathead River–Lake ecosystem, Montana. I. Occasional Paper No. 10, Univ. Montana Biological Station, Bigfork, MT. 152 p.

STANFORD, J. A., AND J. V. WARD. 1979. Stream regulation in North America, p. 215–236. *In* J. V. Ward and J. A. Stanford [ed.] The ecology of regulated streams. Plenum Press, New York, NY. 398 p.

STRAHLER, A. N. 1957. Quantitative analysis of watershed geomorphology. Trans. Am. Geophys. Union 38: 913–920.

VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL, AND C. E. CUSHING. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37: 130–137.

WALLACE, J. B. 1975. Food partitioning in net-spinning Trichoptera larvae: *Hydropsyche venularis*, *Cheumatopsyche etrona* and *Macronema zebratum* (Hydropsychidae). Ann. Entomol. Soc. Am. 68: 463–472.

WALLACE, J. B., J. R. WEBSTER, AND W. R. WOODALL. 1977. The role of filter feeders in flowing waters. Arch. Hydrobiol. 79: 506–532.

WARD, J. V., AND R. A. SHORT. 1978. Macroinvertebrate community structure of four special lotic habitats in Colorado, U.S.A. Verh. Int. Verein. Limnol. 20: 1382–1387.

WARD, J. V., AND J. A. STANFORD. 1979. Ecological factors controlling stream zoobenthos with emphasis on thermal modification of regulated streams, p. 35–55. *In* J. V. Ward and J. A. Stanford [ed.] The ecology of regulated streams. Plenum Press, New York, NY. 398 p.

1982a. Thermal responses in the evolutionary ecology of aquatic insects. Annu. Rev. Entomol. 27: 97–117.

1982b. The serial discontinuity concept of lotic ecosystems. *In* T. D. Fontaine and S. M. Bartell [ed.] Dynamics of lotic ecosystems. Ann Arbor Science Publ., Ann Arbor, MI. (In press)

WIGGINS, G. B., AND R. J. MACKAY. 1978. Some relationships between systematics and trophic ecology of neararctic aquatic insects, with special reference to Trichoptera. Ecology 59: 1211–1220.

Effect of Growth Rate and Size of Fish on Rate of Intoxication by Waterborne Lead

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Three experiments were undertaken to test the null hypotheses that increasing fish size and growth rate do not increase the rate of intoxication of fish by lead. The first experiment demonstrated that there were no significant correlations between weight of fish and either whole-body or blood lead concentrations in feral lake trout (*Salvelinus namaycush*). The whole-body lead concentration of rainbow smelt (*Osmerus mordax*) was, however, negatively correlated to wet weight.

During the second experiment, an 8-d laboratory exposure of rainbow trout (*Salmo gairdneri*) to 100 μg/L of total waterborne lead caused a greater uptake of lead by opercular bone in small fish than in larger fish. No relationship was apparent between fish weight and uptake of lead by blood.

Chronic exposure of juvenile rainbow trout to lead results in the development of black tails, a symptom of neurotoxicity. The final experiment related the incidence and prevalence of black tails to size and growth rate (ration level) of juvenile rainbow trout chronically exposed to 543 μg/L of total waterborne lead starting with the sac-fry stage. At weights below a common threshold size of 1.5–2.5 g, no black tails occurred; above this threshold the incidence of black tails was a function of growth rate, i.e. the rate at which fish reached the threshold size. The prevalence of black tails was always less in slowly growing fish.

These experiments demonstrated that the rate of intoxication by lead, as indicated by uptake rates into tissues and the incidence and prevalence of a symptom of neurotoxicity, did not increase with fish size, but rather with growth rate.

Key words: fish, toxicity, lead, fish size, growth rate, neurotoxicity, uptake

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Les expériences décrites dans le présent article furent menées en vue de tester les hypothèses nulles que l'augmentation de taille et de taux de croissance des poissons n'accélère pas leur taux d'intoxication par le plomb. La première expérience démontre qu'en l'absence

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de corrélations significatives entre le poids des poissons et les concentrations de plomb, soit dans le corps entier soit dans le sang, chez des touladis (*Salvelinus namaycush*) retournés à l'état sauvage. La concentration de plomb dans le corps entier d'éperlan (*Osmerus mordax*) est toutefois en corrélation négative avec le poids humide.

Dans une deuxième expérience, une exposition de truites arc-en-ciel (*Salmo gairdneri*) de 8 jours en laboratoire à 100 μg/L de plomb total dans l'eau résulte en une plus grande absorption de plomb par l'os operculaire chez les petits poissons que chez les grands. Il n'y a pas de relation apparente entre le poids des poissons et l'absorption de plomb par le sang.

L'exposition chronique de jeunes truites arc-en-ciel résulte en la formation de queues noires, un symptôme de neurotoxicité. Dans une dernière expérience, nous avons étudié l'incidence et la prédominance de queues noires en relation avec la taille et le taux de croissance (niveau de ration) de jeunes truites arc-en-ciel soumises à une exposition chronique de 543 μg/L de plomb total dans l'eau, depuis le stade d'alevin vésiculé. À des poids inférieurs à une taille de seuil commune de 1,5−2,5 g, il ne se produit pas de queues noires. Au-delà de ce seuil, l'incidence de queues noires est fonction du taux de croissance, c.-à.d. du taux auquel les poissons atteignent la taille de seuil. La prédominance de queues noires est toujours moindre chez les poissons à croissance lente.

Ces expériences démontrent que le taux d'intoxication par le plomb, tel qu'indiqué par les taux d'absorption par les tissus et l'incidence et la prédominance d'un symptôme de neurotoxicité, n'augmente pas en fonction de la taille du poisson, mais plutôt en fonction du taux de croissance.

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WHEN rainbow trout (*Salmo gairdneri*) or brook trout (*Salvelinus fontinalis*) are continuously exposed to chronically toxic concentrations of waterborne lead, starting at the egg stage, they develop the following symptoms: (a) "black tails," a darkening of the caudal area behind the dorsal fin, usually followed by spinal curvature; (b) elevated concentrations of lead in tissues; and (c) inhibition of the erythrocyte enzyme, δ-aminolevulinic acid dehydratase (ALA-D) (Davies et al. 1976; Holcombe et al. 1976; Hodson et al. 1979, 1980). The development of black tails, a symptom of neurotoxicity, occurs within 6−7 wk of the onset of feeding (Hodson 1979). We have observed repeatedly that, within any group, the larger fish develop black tails first (unpublished data). Thus, the rate of lead poisoning could be a function of either size or growth rate of the fish. Lead uptake and/or the effect of accumulated lead should, therefore, increase either with fish size or with ration level, for a given exposure.

Three experiments were conducted to test the null hypotheses that neither increasing fish size nor growth rate affects the rate of intoxication of fish by lead. The lead concentrations in tissues of different-sized fish were compared in experiments 1 (feral fish) and 2 (laboratory fish) to determine whether a positive relationship existed between fish weight and tissue lead concentrations. The assumption was that observed positive correlations between lead exposure, lead content of tissues, and degree of intoxication (Hodson et al. 1978, 1980) would allow prediction of variations in lead toxicity with size. The third experiment related the incidence (number of new cases per week) and prevalence (total number of cases at any time) of black tails to the growth rates and sizes of trout fed at different rates during a laboratory exposure to waterborne lead.

Materials and Methods

EXPERIMENT 1

Lake trout (*Salvelinus namaycush*) and rainbow smelt (*Osmerus mordax*) were gillnetted by Ontario Ministry of Natural Resources personnel during a 3-wk period (July−August, 1979) from stations in Lake Ontario (Fig. 1). After determination of length, weight, and sex, the carcasses of 25−50 lake trout from each of four stations (n = 166) were wrapped in hexane-rinsed aluminum foil for later individual whole-body lead analysis, as were 4−10 pooled samples of five smelt per sample from each of three stations (n = 22). Whole-body total lead concentrations were measured by the method of Chau et al. (1980) using U.S. National Bureau of Standards Bovine Liver SRM #1577 as a control sample throughout. Repetitive analysis (n = 7) of this standard reference material produced a mean and standard deviation of 386 ± 30 ng Pb/g, which was not significantly different from the accepted value of 340 ± 80 ng/g dry weight. Blood was collected from the caudal artery of 10−20 lake trout subsampled at each station and analyzed for lead content (n = 58) and erythrocyte ALA-D activity (n = 62) (Hodson et al. 1977). Detection limits for the blood and whole-body lead analyses were 10 μg/L and 30 μg/kg wet weight, respectively.

Correlation coefficients were calculated for the linear relationships of the three measures of tissue lead to weight, and the statistical significance of the slopes and correlations was tested at the 0.05 probability level (Steel and Torrie 1960). As all data conformed to normal distributions and the variance was independent of the means, no transformations were

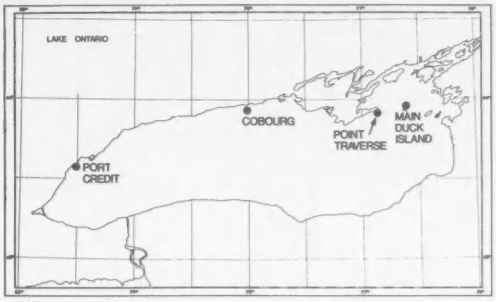

FIG. 1. Sampling locations in Lake Ontario for lake trout (*Salvelinus namaycush*) and smelt (*Osmerus mordax*).

necessary (Steel and Torrie 1960). The lead exposure of free-ranging fish could obviously not be measured, but was assumed to be the same for all fish within a species at any sampling station, based on schooling behavior. Reported mean total lead concentrations in filtered water samples from Lake Ontario range from <0.3 to 0.8 μg/L (International Joint Commission 1980).

EXPERIMENT 2

The effect of size on lead uptake by rainbow trout exposed to a nominal concentration of 100 μg/L of waterborne lead was tested by a factorial experiment. Mean weights (±SD) of the 36 fish in each of the three size-classes tested were as follows: small, 11.0 ± 3.4 g; medium, 69 ± 20.8 g; and large, 296 ± 51.9 g. At the time of the study, the fish were 5, 17, and 20 mo old, respective to size categories. The fish were exposed to lead for 0, 0.5, 1, 2, 4, or 8 d. The experiment was conducted three times (three replicates) with two fish of each size sampled at each exposure time for each replicate; the total sample size was 108 (3 sizes × 6 times × 2 fish × 3 replicates).

Rainbow trout eggs were purchased from Norfolk Trout Fisheries, Simcoe, Ontario, and reared in the laboratory in Lake Ontario water at a pH of 7.8 and a total hardness of 135 mg/L (as $CaCO_3$). Fish were fed a commercial trout diet at the levels recommended for hatchery production (Brown and Gratzek 1980). A photoperiod of 16 h light − 8 h dark and a temperature of 15°C were maintained before and during experimentation. Growth of medium fish was slowed at 12−16 mo of age by rearing at 5°C.

Lead exposure was carried out in 45-L glass tanks (46 cm long × 35 cm wide × 28 cm high) subdivided by plastic grids (1 cm^2 mesh) to provide an individual compartment for each fish. Tanks were subdivided into six cells for small fish and two cells for medium fish, whereas each large fish had a tank to itself. The inflowing water, aeration, and fish movement ensured adequate mixing within each tank. Flows were maintained at 200 mL/min per tank which provided daily flows for small, medium, and large fish of 4.4, 2.1, and 1.0 L/g of fish, respectively, and a 95% molecular replacement time in each tank of about 10 h (Sprague 1969). Lead, from a lead nitrate stock solution, was added to the water supply by a peristaltic pump. Total lead concentrations were measured daily by atomic absorption spectrophotometry (Department of Environment 1979) and means (±SD) for the three replicates were 80 ± 9, 90 ± 13, and 122 ± 14 μg/L, respectively. Within any 1 d, the standard deviation of between-tank variability averaged 12.5% of the mean. The three measurements of the effect of size on lead uptake by trout were not confounded by the above variation of waterborne lead. Subsequent analysis of variance (Steel and Torrie 1960) showed no significant size−replicate interactive effects on lead uptake.

Fish to be exposed 8 d were added to a given cell or tank at time 0, fish to be exposed 4 d were added on day 4, and fish to be exposed 1 d were added on day 7. Thus, on a given sampling day, all fish from a particular replicate were sampled simultaneously allowing standardization of sampling and analytical procedures. The order of tanks assigned for small, medium, and large fish was randomized, as was the order in which fish were removed on day 8. Fish were selected for exposure by netting a large number from a stock tank and assigning individual fish to treatment tanks by stratified distribution. Fish were not fed during the 8-d lead exposure.

On each sampling day, measurements of blood lead concentration, erythrocyte ALA-D activity (Hodson et al. 1977), and standard length and weight of fish were made. Opercular bones were removed from the fish of the third replicate, frozen, and later analyzed for lead content (Hodson et al. 1978).

Results for each variable measured were analyzed by factorial analysis of variance at the 0.05 probability level (Steel and Torrie 1960). Statistically significant interactions between experimental measurements and fish size or time were the criteria for a positive size effect on rate of lead uptake.

EXPERIMENT 3

Rainbow trout from Goossen's Trout Farm Ltd., Otterville, Ontario, were exposed to lead for a 14-wk period starting at the sac-fry stage, 2 wk prior to swim-up. Starting at swim-up (average weight = 0.11 g), fish were fed Silver Cup Juvenile salmon diet (Murray Elevators, Murray, Utah) at one of three ration levels, designated as low, medium, or high (Table 1). Each treatment was carried out in triplicate, for a total of 18 tanks (3 rations × 2 lead exposure levels × 3 replicates). Parameters measured were percentage mortality, growth, prevalence and incidence of black tails, and weight at the onset of black tails. At the end of the experiment, five fish from each tank were sampled for standard length, weight, blood lead concentration, and activity of erythrocyte ALA-D (Hodson et al. 1977).

The experiment was carried out in University of Guelph well water, characterized by Dixon and Sprague (1981). In-tank temperatures were maintained at 11.6 ± 0.2°C (n = 42) during sac resorption and until 1 wk after swim-up to promote survival. Subsequently, the mean temperature was raised by 1° per day to 15.0 ± 0.2°C (n = 84) to promote growth. The mean dissolved oxygen level of 8.6 ± 0.3 mg/L (n = 38) represented 86% saturation. The mean pH was 8.03 ± 0.07 (n = 14) and the mean total hardness (as $CaCO_3$) was 385 ± 2.1 mg/L (n = 14). Photoperiod was maintained at

TABLE 1. Ration levels given to juvenile rainbow trout during a 14-wk exposure to 0 or 543 μg/L of total waterborne lead.

Fish size (g)	Feeding rate (as % of highest level)	Ration level (weight of food given per day as % of wet weight biomass)	Feed particle size
0.1–0.2	100 (high)	6.0	Starter
	80 (intermediate)	4.8	
	60 (low)	3.6	
0.2–1.5	100 (high)	5.8	1,2
	80 (intermediate)	4.6	
	60 (low)	3.5	
1.5–5.1	100 (high)	4.5	2,3
	80 (intermediate)	3.6	
	60 (low)	2.7	
5.1–12.0	100 (high)	3.5	4
	80 (intermediate)	2.8	
	60 (low)	2.1	

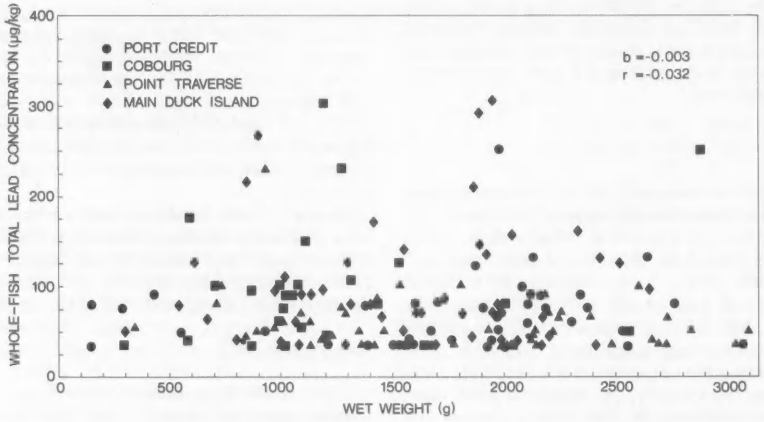

FIG. 2. The variation of whole-body lead concentrations with weight of lake trout (*Salvelinus namaycush*) sampled at four locations in Lake Ontario. The relationship was not statistically significant (correlation coefficient = −0.03, $P < 0.05$).

16 h of light and 8 h of darkness.

Fish were exposed to lead in an 18-tank continuous-flow apparatus. A flowmeter regulated a stream of control water from a constant-head tank, while a parallel stream was mixed with a lead nitrate stock solution from a Mariotte bottle (Leduc 1966). Each stream reached the tanks through nine-way flow splitters patterned after the "Chadwick" diluter described by Weinstein (1978). Lead concentrations in samples taken daily from at least one toxicant-treated tank were measured by atomic absorption spectrophotometry (Department of Environment 1979). The mean total lead concentration was 543 ± 21 μg/L (n = 97), 90.5% of the 600 μg/L nominal value. This concentration was chosen to ensure appearance of symptoms of lead toxicity within a reasonable time, based on the hardwater data of Davies et al. (1976). The volume of each 20-L cylindrical polyethylene exposure tank was adjusted to 18 L with a standpipe. Each tank received water at a rate of 273 ± 11 mL/min (n = 61) for a 95% molecular replacement time of 3.5 h (Sprague 1969). Tanks were gently aerated and covered with translucent polyethylene lids.

The experiment started when 250 sac-fry were randomly assigned to each tank. The total biomass in each tank was determined weekly by weighing all fish together and it was used as a measure of growth and to adjust ration level and feed-particle size (Table 1). The number of fish with black tails was recorded weekly. Fish showing black tails for the first time were weighed individually, a pectoral fin was clipped to eliminate repeat weighings, and they were returned to their respective tanks. Based on a flow rate of 3 L of water per gram of fish per day (Sprague 1969), each tank was capable of sustaining a maximum biomass of 120 g and the biomass was reduced biweekly to maintain that limit. When black tails were present, black tail and normal fish were removed proportionally and impartially without regard to size.

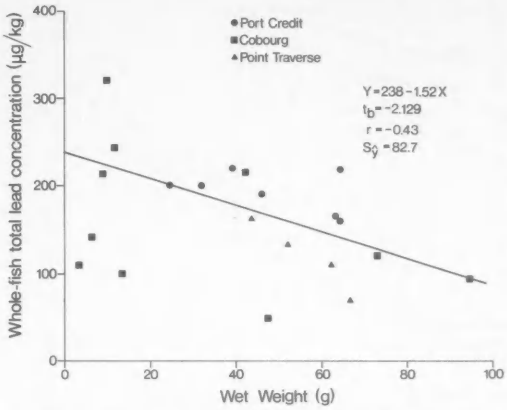

FIG. 3. The variation of whole-body lead concentrations with weight of smelt (*Osmerus mordax*) sampled at three locations in Lake Ontario. The relationship was statistically significant (correlation coefficient = −0.43, $P > 0.05$).

Analysis of variance and Duncan's new multiple range test were used to assess the statistical significance of treatment effects on incidence of mortality, incidence and prevalence of black tails, mean weight at onset of black tails, blood lead concentration, and ALA-D activity (Steel and Torrie 1960). Effects on growth were determined by regressing $\log_{10}$ of mean weight on time for each of the 18 replicates, and comparing the slopes of the regression lines by analysis of variance (Steel and Torrie 1960). The statistical significance of these results was assessed at the 0.05 probability level.

Results

EXPERIMENT 1

There were no obvious relationships between wet weight and whole-body lead concentrations, blood lead concentrations, and erythrocyte ALA-D activities of lake trout. Figure 2 illustrates the data for whole-body lead content. Many of the observations were at the limit of detection but even if the true lead concentration were known, it is unlikely that these low values would establish a relationship to wet weight as they were spread throughout the weight range. The correlation coefficients for the regression of whole-body lead concentration, blood lead concentration, and ALA-D activity on wet weight were −0.03, 0.03, and −0.17, respectively.

In contrast, the whole-body lead concentration of smelt was negatively correlated to wet weight (Fig. 3). The slope was statistically significant at the 0.05 probability limit ($t_{0.025,20} = 2.129$, $P < 0.05$) but the relationship may be strongly affected by the small sample size ($n = 22$) and several extreme points (Fig. 3).

EXPERIMENT 2

Lead concentrations in the blood and opercular bone and the percentage inhibition of ALA-D increased with time in all sizes of rainbow trout exposed to lead for 8 d (Fig. 4). ALA-D inhibition was independent of weight ($F_{2,53} = 1.5096$, $P > 0.05$) but blood lead concentrations varied with weight ($F_{2,53} = 6.449$, $P < 0.05$). However, the *rate* of lead accumulation by blood did not vary with weight, nor was there a positive correlation of blood lead to fish weight (Fig. 4). Weight had a significant negative effect on opercular bone lead concentrations, i.e. small fish had higher concentrations than large (Fig. 4) ($F_{2,17} = 4.9732$, $P < 0.05$). Blood lead concentrations and ALA-D inhibition approached equilibrium with waterborne lead by 8 d exposure whereas lead concentrations in opercular bone were still increasing after 8 d.

EXPERIMENT 3

Neither lead exposure ($F_{1,12} = 1.76$, $P > 0.05$) nor ration level ($F_{2,12} = 0.55$, $P > 0.05$) had a significant effect on incidence of mortality, which was one to six fish per 1000 fish-days per replicate during the first 5 wk, and zero during the remainder of the study. Although growth was affected significantly by ration level ($F_{2,12} = 5.33$, $P < 0.05$), it was not affected by lead exposure ($F_{1,12} = 0.29$, $P > 0.05$) nor by exposure-ration level interactions ($F_{2,12} = 1.00$, $P > 0.05$). Final mean weights of the fish, from high to low ration level, were 10.3 ± 1.4, 7.4 ± 1.1, and 5.3 ± 0.8 g (Fig. 5).

Rainbow trout exposed to lead from the sac-fry stage developed black tails, whereas control fish did not. During the exposure, faster growing fish developed black tails earlier than did slower growing fish (Fig. 6). At both high and intermediate ration levels, black tails first appeared 4 wk after swim-up and by the 6th wk, 38% of the fish at the high ration level and 47% at the intermediate ration level were affected. Although these proportions were significantly different ($F_{2,6} = 35.6$, $P < 0.05$), those for weeks 7 through 12 after swim-up were not. In contrast, fish on the low ration level did not exhibit black tails until week 7, and the prevalence was always significantly lower than that observed at the intermediate and high ration levels ($F_{2,6} = 10.10$, $P < 0.05$). By 12 weeks after swim-up, prevalence from high to low ration level was 82 ± 4, 85 ± 5, and 66 ± 8%, respectively (Fig. 6). A plot of the incidence of black tails (new cases per week) shows that the populations on high and medium ration levels had similar peaks at 6 wk exposure, after which the incidence declined (Fig. 7B). Fish on the low ration level, however, had two peaks of response at 7 and 9−10 wk and the incidence did not decline as rapidly as at the two higher ration levels. When these data were compared with fish weights to eliminate the growth rate difference from the comparison, all three groups had a peak of response between 1.5 and 2.5 g wet weight. Fish on the low ration level had a secondary peak at 3−4 g (Fig. 7A).

Mean weights of fish at the onset of black tail, from high to low ration level, were 2.53 ± 0.21, 1.99 ± 0.16, and 2.35 ± 0.22 g, respectively. The mean weight at the onset of black tail for the intermediate ration was significantly lower ($F_{2,6} = 13.18$, $P > 0.05$) than the other two, which were not significantly different from each other.

There were no significant differences between the blood

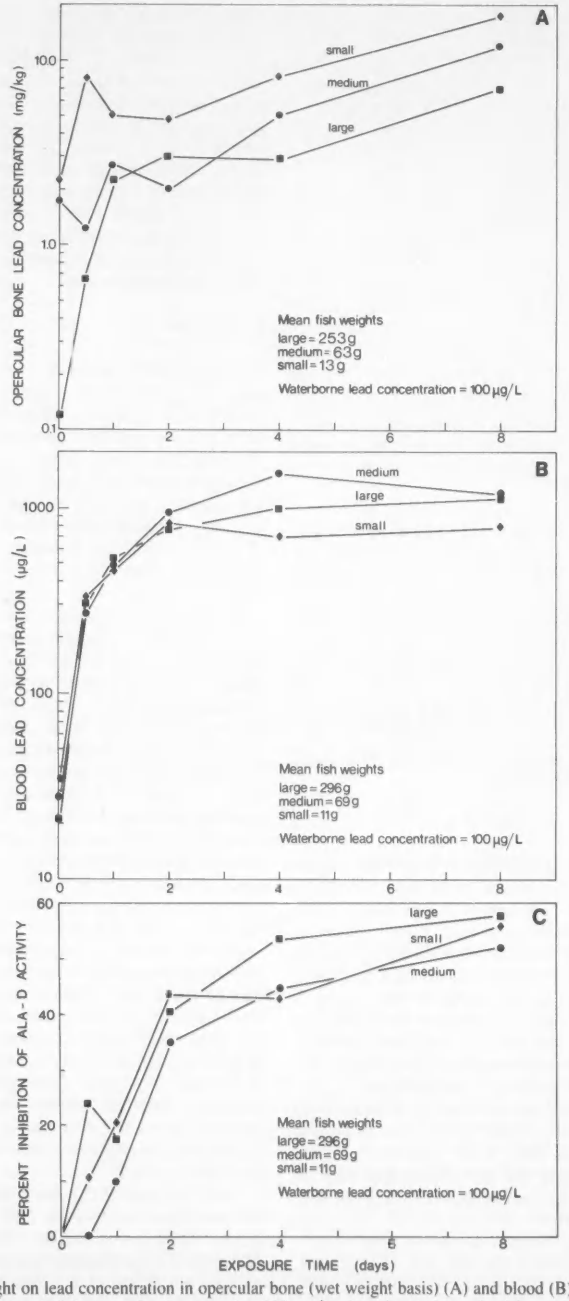

FIG. 4. The effect of fish weight on lead concentration in opercular bone (wet weight basis) (A) and blood (B), and percentage inhibition of ALA-D activity (C) of rainbow trout (*Salmo gairdneri*) exposed to 100 µg/L of total waterborne lead for periods of up to 8 d. The standard deviations (calculated from the pooled error variance of the analyses of variance) of opercular bone lead concentrations, blood lead concentrations, and percentage inhibition of ALA-D activity were 3.1 mg/kg, 256 µg/L, and 12.8%, respectively. The logarithm of mean tissue lead concentrations was plotted to allow a more convenient data presentation.

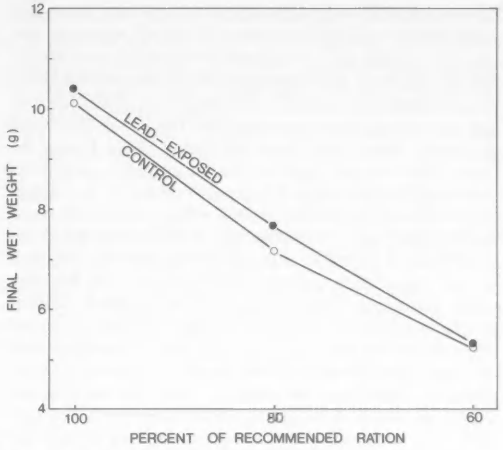

FIG. 5. Final mean weights attained by rainbow trout fed on low, intermediate, or high ration levels during exposure to 0 or 574 μg/L of total waterborne lead.

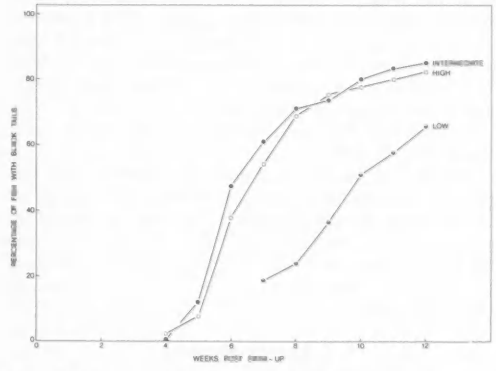

FIG. 6. Prevalence of black tails in rainbow trout fed on high, intermediate, or low ration levels during exposure to 574 μg/L of total waterborne lead. Each point is the mean of three replicates. Control results are not given, as no control fish developed black tails.

lead and ALA-D values of lead-exposed fish on the three diets at the end of the experiment. The mean blood lead concentrations of fish on high, medium, and low ration levels were 468 ± 148, 438 ± 158, and 459 ± 143 μg/L, respectively. Linear regression analyses of ALA-D activity on $\log_{10}$ blood lead concentrations showed that high, medium, and low rations had no effect on slopes (−76 ± 22, −50 ± 18, and −60 ± 17, respectively) or *Y*-intercepts (398 ± 80, 371 ± 68, and 360 ± 45 nmol PBG per millilitre RBC per hour, respectively).

Temporary scoliosis, an additional symptom of lead neurotoxicity, occurred in some fish during this experiment. When fish on the intermediate ration level were subjected to the stress of weighing during the second half of the study,

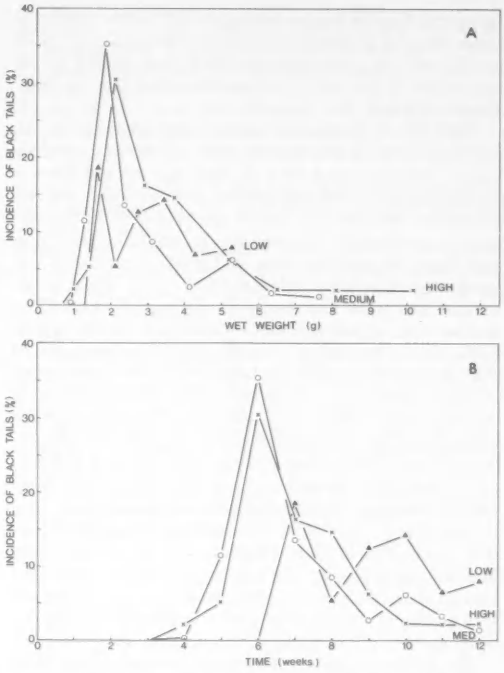

FIG. 7. Incidence of black tails versus time (A) and weight (B) in rainbow trout fed high, intermediate, or low ration levels during exposure to 574 μg/L of total waterborne lead.

5−10% developed scoliosis which was sustained for 0.5−1.5 h. This did not occur in fish on high and low ration levels, and none of the fish developed permanent scoliosis during this experiment.

Discussion

These experiments have demonstrated the following: (a) whole-body and blood lead concentrations of lake trout did not vary with weight but whole-body lead concentrations of smelt varied inversely with weight; (b) the rate of lead uptake by the blood of rainbow trout during exposure to waterborne lead did not vary with weight. In contrast, opercular bones of small fish accumulated lead to a greater extent than did those of large fish; and (c) the rate of appearance of black tails in lead-exposed juvenile rainbow trout was a function of growth rate rather than fish size.

Chronic lead toxicity to trout increases with tissue lead concentrations (Hodson et al. 1978; Holcombe et al. 1976). Therefore, one cause of increased sensitivity of fish to lead could be increased tissue accumulations. If large fish are more sensitive to lead than small fish, they may accumulate more lead than small fish. The first experiment demonstrated that lead concentrations did not increase with size and the opposite was the case with smelt. However, this experiment was inconclusive as the actual lead exposure of feral fish could not be

measured. Overall lead residues were quite low relative to those observed in laboratory exposures (Hodson et al. 1978) so that lead accumulations may have been limited by the availability of lead in the environment rather than by variations in fish size.

The results of the second experiment also supported the null hypothesis that fish size does not affect the rate of lead intoxication. Neither uptake rates of lead into the blood nor a biological response to blood lead (ALA-D inhibition) was size dependent. However, the rate of opercular bone lead uptake was size dependent with small fish accumulating lead faster than large. As opercular bone lead uptake is typical of lead uptake by other tissues (Hodson et al. 1978), these results indicate that small fish should show signs of chronic lead toxicity more quickly than do larger fish, a situation opposite to that seen in this and past experiments. However, the blood lead concentration equilibrated rapidly with waterborne lead. As lead in the blood is the primary source of uptake by other internal tissues, rates of lead uptake by these tissues will be a function of the concentration in the blood which is independent of size. The volume of whole fish increases with size faster than does their blood volume (Holmes and Donaldson 1969). Therefore, at a constant rate of uptake, individual tissues of large fish will take longer to equilibrate with blood than those of small fish. Consequently, short-term uptake rates by specific tissues may vary inversely with fish size, but long-term equilibrium concentrations should not. As chronic lead toxicity is a result of long-term lead exposures, the rate of appearance of black tails should not vary with fish size.

This conclusion appears to contradict several studies showing a well-defined mathematical relationship between toxicity and fish size (Mount 1962; Anderson and Weber 1975; Howarth and Sprague 1978). In general, these studies have demonstrated an inverse relationship between acute lethality and weight. However, in short-term tests typical of the experiments cited above, results from the present experiment indicate that target tissues will acquire a toxic load of contaminant sooner in small fish than in large. The equations relating acute toxicity to fish size could in fact describe the effect of size on tissue uptake rates. Therefore these results might not be contradictory as the size/toxicity relationship may apply only to short-term acute lethality and not to chronic toxicity; in cases of chronic exposure, tissue residues should reach equilibrium, regardless of size, long before symptoms of toxicity are evident.

The results of the third experiment showed that trout chronically exposed to lead exhibited no symptoms of lead toxicity until they reached a size of 1.0 g, after which the incidence of black tails increased and peaked rapidly (Fig. 7A). Ration level did not affect blood lead concentrations after 12 wk of growth which indicated that lead uptake was independent of growth rate. There seems to be a size threshold that governs the response to lead so that the rate of lead intoxication (or appearance of symptoms) is a function of how quickly the fish reach the threshold size. As lead did not affect growth rates, time to the first black tails can be roughly predicted from control growth rates at any ration level.

The occurrence of black tails may be related to growth rate in other ways, as the prevalence of black tails varied with ration level at a given size. For example, at a mean size of 5 g, the prevalence of black tails was 70, 74, and 56% at the high, medium, and low ration levels, respectively. There are two possible explanations of this ration level effect. The first is that the threshold size-relationship has been confounded by growth depensation (spread in fish weights). Growth depensation increases as ration level decreases due to aggression and dominance hierarchies (Eaton and Farley 1974). If only the larger fish in a tank have the black tail symptom, the high depensation at low ration levels may provide a false indication of the weight/prevalence relationship. The second explanation is that the rate of intoxication is a function of both the growth rate of the target tissue, the spinal neurons, and their rate of repair. Lead-poisoned fish transferred to lead-free water regain color control myomere by myomere (unpublished observations), which may represent neuronal repair and regeneration. As regeneration should proceed from the central cell body towards the periphery, it would take longer for a neuron to regenerate in an actively growing lead-exposed fish than in one which is elongating slowly. Therefore, it appears that repair rates in slowly growing fish exposed to lead may be more nearly in balance with the rate of neuronal destruction than in quickly growing fish.

The threshold size for appearance of black tails suggests that some critical minimum target tissue size or stage of development must be reached before lead intoxication causes sufficient damage to produce this symptom. The occurrence of this pathology is not simply size dependent but is a function of age and requires continuous pre-exposure to lead. Trout are much less sensitive to lead when exposure is initiated at an age of 4 mo (inferred from Hodson et al. 1978) compared with those exposed continuously from hatch (Hodson et al. 1979).

In summary, the results of these experiments do not support the null hypothesis that "growth rate of fish does not affect the rate of lead intoxication," but they do support the alternative null hypothesis that "fish size does not affect the rate of lead intoxication." Therefore the toxic effects of lead uptake by fish will be greater in conditions favoring their rapid growth.

Acknowledgments

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ANDERSON, P. D., AND L. J. WEBER. 1975. Toxic response as a quantitative function of body size. Toxicol. Appl. Pharmacol. 33: 471–483.

BROWN, E. E., AND J. B. GRATZEK. 1980. Fish Farming Handbook. The AVI Publishing Co. Ltd., Westport, CT. 391 p.

CHAU, Y. K., P. T. S. WONG, O. KRAMER, G. A. BENGERT, R. B. CRUZ, J. O. KINRADE, AND J. C. VAN LOON. 1980. Occurrence of tetraalkyllead compounds in the aquatic environment. Bull. Environ. Contam. Toxicol. 24: 265–269.

DAVIES, P. H., J. P. GOETTL JR., R. F. SINLEY, AND N. F. SMITH. 1976. Acute and chronic toxicity of lead to rainbow trout, *Salmo gairdneri*, in hard and soft water. Water Res. 10: 199–206.

DIXON, D. G., AND J. B. SPRAGUE. 1981. Acclimation-induced changes in toxicity of arsenic and cyanide to rainbow trout, *Salmo gairdneri* Richardson. J. Fish. Biol. 18: 579–589.

DEPARTMENT OF ENVIRONMENT. 1979. Analytical Methods Manual. Water Quality Branch, Inland Waters Directorate, Environment Canada, Ottawa, Canada.

EATON, R. C., AND R. O. FARLEY. 1974. Growth and the reduction of depensation of zebrafish, *Brachydanio rerio*, reared in the laboratory. Copeia 1974: 204–209.

HODSON, P. V. 1979. Factors affecting the sublethal toxicity of lead to fish, p. 135–138. Proceedings of the International Conference on Management and Control of Heavy Metals in the Environment, London, U.K. Sept. 18–21, 1979. CEP Consultants, Edinburgh, U.K.

HODSON, P. V., B. R. BLUNT, D. JENSEN, AND S. MORGAN. 1979. Effects of fish age on predicted and observed chronic toxicity of lead to rainbow trout in Lake Ontario water. J. Great Lakes Res. 5: 84–89.

HODSON, P. V., B. R. BLUNT, AND D. J. SPRY. 1978. Chronic toxicity of waterborne and dietary lead to rainbow trout (*Salmo gairdneri*) in Lake Ontario water. Water Res. 12: 869–878.

HODSON, P. V., B. R. BLUNT, D. J. SPRY, AND K. AUSTEN. 1977. Evaluation of erythrocyte δ-amino levulinic acid dehydratase activity as a short-term indicator in fish of a harmful exposure to lead. J. Fish. Res. Board Can. 34: 501–508.

HODSON, P. V., J. W. HILTON, B. R. BLUNT, AND S. J. SLINGER. 1980. Effects of dietary ascorbic acid on chronic lead toxicity to young rainbow trout (*Salmo gairdneri*). Can. J. Fish. Aquat. Sci. 37: 170–176.

HOLCOMBE, G. W., D. A. BENOIT, E. M. LEONARD, AND J. W. MCKIM. 1976. Long-term effects of lead exposure on three generations of brook trout (*Salvelinus fontinalis*). J. Fish. Res. Board Can. 33: 1731–1741.

HOLMES, W. M., AND E. M. DONALDSON. 1969. The body compartments and the distribution of electrolytes, p. 1–90. *In* W. S. Hoar [ed.] Fish Physiology. Vol. 1. Academic Press, New York. 461 p.

HOWARTH, R. S., AND J. B. SPRAGUE. 1978. Copper lethality to rainbow trout in waters of various hardness and pH. Water Res. 12: 455–462.

INTERNATIONAL JOINT COMMISSION. 1980. Report of the Aquatic Ecosystems Objectives Committee of the Great Lakes Science Advisory Board. International Joint Commission, Regional Office, Windsor, Ont. 127 p.

LEDUC, G. 1966. Une bouteille à débit constant pour petits volumes de liquides. Naturaliste Can. 93: 61–64.

MOUNT, D. I. 1962. Chronic effects of endrin on bluntnose minnows and guppies. U.S. Fish Wildl. Serv. Res. Rep. 58: 1–38.

SPRAGUE, J. B. 1969. Measurement of pollutant toxicity to fish. I. Bioassay methods for acute toxicity. Water Res. 3: 793–821.

STEEL, R. G. D., AND J. H. TORRIE. 1960. Principles and procedures of statistics. McGraw-Hill, New York, NY. 481 p.

WEINSTEIN, N. L. 1978. Multiple toxicity assessment for mixtures of aquatic pollutants. M.Sc. thesis, Concordia University, Montreal, Que. 116 p.

Discount Factors and Risk Aversion in Managing Random Fish Populations

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MENDELSSOHN, R. 1982. Discount factors and risk aversion in managing random fish populations. Can. J. Fish. Aquat. Sci. 39: 1252–1257.

The effects of changes in the discount factor as compared with the effects of changes in risk aversion are examined for a simple stochastic model of fish population dynamics. Numerical results suggest that both optimal harvesting strategies and the resulting population dynamics are insensitive to changes in the discount factor, whereas changes in the degree of risk aversion in the utility function do cause significant changes in both. When risk averse utility functions are viewed as total revenue curves with marginal prices that decrease with supply, the results suggest that the more sensitive price is to supply, then the resulting optimal harvesting policy is smoother. Theoretical results are presented which suggest these results are robust beyond the specific model.

Key words: discount factors, risk aversion, population dynamics, randomness

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Nous analysons, sur un modèle stochastique simple de dynamique des populations, les effets de changements du facteur escompte comparativement aux effets de changements du facteur aversion contre le risque. Les résultats donnent à penser que les stratégies de récolte optimale, ainsi que la dynamique des populations qui en résulte, ne sont pas influencées par les changements du facteur escompte. Par contre, le degré d'aversion contre le risque dans la fonction utilité entraîne en fait des changements significatifs dans les deux. Quand on considère les fonctions utilité opposées au risque en termes de courbes de revenus totaux, avec prix marginaux qui diminuent en même temps que l'offre, les résultats suggèrent que plus le prix est sensible à l'offre et plus douce est la politique de récolte optimale qui en découle. Nous présentons des résultats théoriques vraisemblablement applicables au-delà de ce modèle particulier.

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THE standard literature (see Clark 1976, 1980; Anderson 1977; and references therein) on dynamic, deterministic fishery optimization models has stressed the importance of the discount factor $(1/(1 + i)$, where i is the interest rate) in determining optimal harvesting strategies. The discount factor has been emphasized because an optimal harvesting strategy depends continuously on the discount factor, and a stock will be optimally harvested to extinction if the rate of growth of the population is less than the rate of discount (Reed 1974; Clark 1976). Related results have been established for stochastic harvesting models (Reed 1974; Mendelssohn 1980b; Mendelssohn and Sobel 1980), though in a stochastic model the population dynamics may drive the population to extinction even though the harvest levels have not left the remaining population at or near zero.

The presumed sensitivity of an optimal harvesting strategy to changes in the discount factor is important, as a standard procedure for representing increased risk to a manager of a fishery in face of uncertainty is to decrease the discount factor. Even at first glance this is a naive approach, as it assumes a constant attitude towards risk regardless of the initial population size or harvest decision.

What would appear to be a more sophisticated approach towards risk is to assess the manager's utility function and use this as the objective function. This approach to managing fisheries and other natural resources is given in Hilborn and Walters (1977), Keeney (1977), and Holling (1978); a general discussion can be found in Keeney and Raiffa (1976).

One way to compare these differing approaches is to see how changes in the discount factor and changes in the degree of risk aversion affect the policy that should be followed. In this paper this is done for one empirical stochastic model of a fishery. In particular, the actual sensitivity of an optimal harvesting strategy to changes in the discount factor is compared with its sensitivity to changes in the degree of risk aversion in the utility function. Further changes in the population dynamics of a stock being managed under an optimal

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harvesting policy are examined as both the discount factor and the degree of risk aversion vary. Also, the appendix presents theoretical results which suggest the numerical results presented are robust over a wide class of models.

The Model

The model to be analyzed is a stochastic version of a Ricker spawner–recruit curve put forward by Mathews (1967) for salmon runs in Bristol Bay. Let x_t be the recruits in period t, and y_t the spawners. If x is observed and a decision y is taken, a one-period utility $g(x, y)$ is received. Without loss of generality, $g(x, y)$ can be the expected value (over the random variable θ) of some other utility $h(x, y, \theta)$. Hence the model indirectly includes economic uncertainty.

The utility in period t is discounted by a factor β, $0 \leq \beta < 1$. The recruits in period $t + 1$ are a random function of the spawners in period t and a random variable d,

$$(1) \quad x_{t+1} = d4.084y_t \exp\{-0.8y_t\}; \ \ln d \sim N(0, 0.2098)$$

where $N(0, \sigma^2)$ denotes a random variable that follows a normal distribution with mean zero and variance σ^2.

The problem is to maximize the expected discounted utility.

$$(2) \quad \text{maximize} \sum_{t=1}^{\infty} \beta^{t-1} g(x_t, y_t)$$

such that $x_t \geq y_t \geq 0$; Eq. (1).

Computational techniques for solving Eq. (2) and related policy questions are discussed in Mendelssohn (1980b). A 100-point grid is used with no absorbing (zero) population size.

Two different utility functions are examined for $g(x, y)$. The first is $v_1 = 0.5 \ln (x_t - y_t)$ while the second is $v_2 = (x_t - y_t)^{\lambda}$, for $\lambda = 0.05, 0.1, 0.25, 0.5, 0.75, 0.9, 0.95, 1.0$. These utility functions are plotted in Fig. 1. Utility functions are said to be absolute risk averse (Merton 1969, 1971; Keeney and Raiffa 1976) if $-u''(z)/u'(z) > 0$ for a function $u(z)$. The Pratt measure of relative risk aversion is $-u''(z)z/u'(z)$. Basically, a utility function is risk averse if a certain return is preferred to a lottery with equal or greater value in expectation.

The two utility functions v_1 and v_2 are members of the HARA (hyperbolic absolute risk averse) family of utility functions (Merton 1969, 1971). In particular, if R_1 is the measure of absolute risk aversion, and R_2 is the measure of relative risk aversion, then for v_1, $R_1 = 1/z$ and $R_2 = 1$; for v_2, $R_1 = (1 - \lambda)/z$ and $R_2 = 1 - \lambda$, where $z = x - y$ is the amount harvested. Both v_1 and v_2 have constant relative risk with respect to the amount harvested. However, it is clear that the relative risk aversion for v_2 changes linearly with λ. Hence λ is a measure of the relative degree of risk aversion. For λ approaching zero, the manager is totally risk averse, whereas for $\lambda = 1$ the manager is risk neutral. The utility function v_1 is the limiting case of v_2 as λ approaches zero.

The utility functions v_1 and v_2 are not as rich as they might be given that they only depend on (x_t, y_t) through $z_t = x_t - y_t$. However, there exists little empirical basis for choosing more complicated utility functions that can be given meaningful, practical interpretations. Both v_1 and v_2 can be viewed as total revenue curves. Taking derivatives $v_{1'} = 0.5/z$ ($v_{2'} = \lambda z^{\lambda-1}$) and $v_{1''} = -0.5/z^2$ (respectively, $(1 - \lambda)z^{\lambda-2}$). The first derivative is the marginal price for a supply of z units of fish, with the marginal price decreasing with increasing supply. Therefore, using v_1 and v_2 as the one-period utility functions can be viewed as examining the effect of dropping the usual economic assumption of perfect competition. This is treated analytically in some detail in Mendelssohn and Sobel (1980).

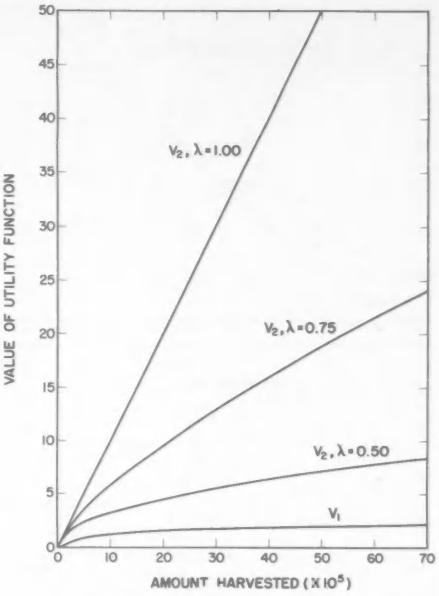

FIG. 1. Graph of the different utilities function.

It is worth emphasizing that "risk" is used here in a very specific way. In some papers, risk is used to denote the randomness in the population dynamics. Here, it is assumed that all random variation in the population is contained in the random variable d. No effort is made to discuss the actual merits or accuracy of Mathew's model. Instead the model is taken as given.

Also, sometimes risk is used to denote undesirable events that could happen to the population that are not directly reflected in the utility function. The risk of extinction or of very small population sizes is one such example. This problem is treated in Mendelssohn (1978).

Risk in this paper denotes the gamble the decision maker faces in the certain reward of the given return function (in this case harvest) this period versus the uncertain return next period. The return function is assumed given. For many problems, the choice of the appropriate return function is crucial (Mendelssohn 1980b).

Results

Optimal harvesting policies and the resulting population

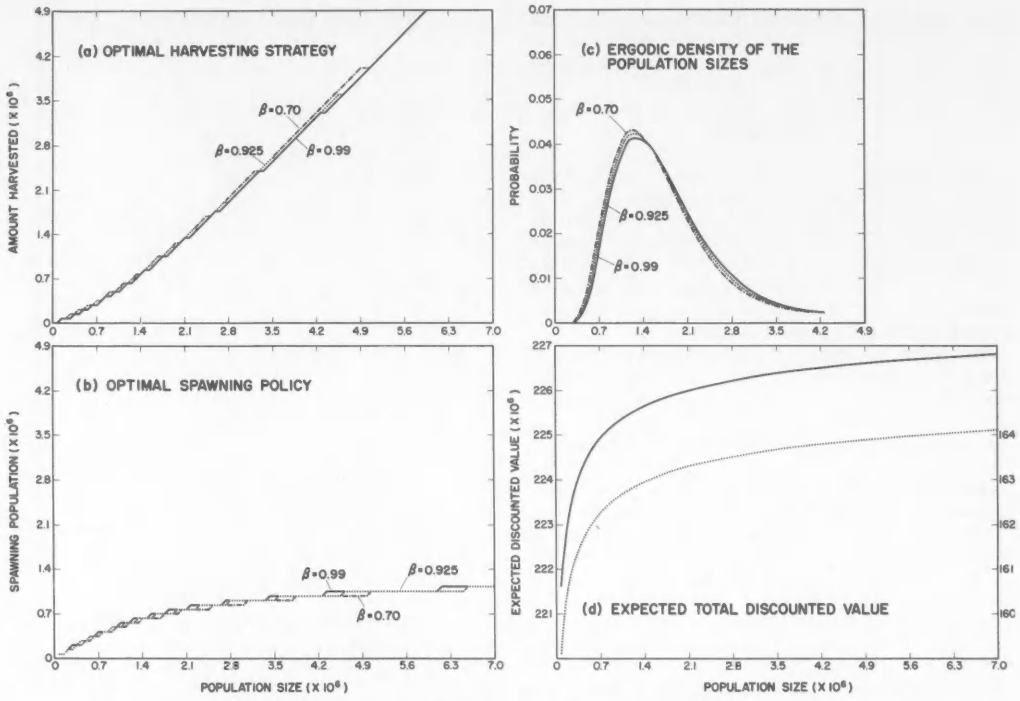

FIG. 2. Effects on an optimal policy and optimal value from varying the discount factor.

dynamics were calculated for both classes of utility functions for discount factors of 0.99, 0.95, 0.925, 0.9, 0.85, 0.80, and 0.70. These discount factors are equivalent to interest rates of 1, 5.23, 8.1, 11.1, 17.65, 25, and 42.86%. Results are shown only for the utility function $v_1 = 0.5 \ln(x - y)$ and several of the extreme values of the discount factor. The results using v_2 with any value of λ are nearly identical to those presented for v_1, and the graphs change uniformly with β, so the graphs in Fig. 2 represent the extreme changes.

Visually it is clear that the curves in Fig. 2 are extremely similar. For the discount factors $\beta = 0.99$ and $\beta = 0.70$ the optimal number of spawners to leave after harvesting agree at 50 out of 100 states and differ by only one grid point at the rest of the states. Moreover, it can be shown that this result remains valid for much finer grids; hence the two policies can be made to be extremely close together.

The long-run (ergodic) population sizes show a slight shift to smaller population sizes as β decreases, but the cumulative ergodic harvest distributions are virtually indistinguishable over the range of discount factors examined.

Figure 2(d) shows an optimal value function, $\sum_{t=1}^{t} \beta^{t-1} v_1(t)$ when starting in each state, for $\beta = 0.99$ and $\beta = 0.925$. Despite the fact that almost identical sample paths are generated by the two optimal harvesting strategies, the change in the valuation of the sample paths is dramatic.

There has been much discussion in the fisheries literature on the appropriate value of the discount factor (Walters 1975; Clark 1976; Walters and Hilborn 1976; Holling 1978). This discussion can be divided into two components—the discount factor that should be used to evaluate the fishery by an external agency such as a government agency (say to compare the benefits derived from a stream enhancement project) or a private individual (when making an entry decision, for example) and that used by the fishery manager to set policy, bearing in mind the effects harvest policy will have on the former decisions. If the previous empirical results are robust, they suggest that the fishery manager need not worry greatly about the exact choice of the discount factor used for determining policy, and that this choice will have little bearing on entry decisions or enhancement projects. This is because a nearly optimal expected present value will be found over a broad range of discount factors that might be used by the external agents.

Figure 3(a–e) shows similar results for the v_2 with $\beta = 0.95$ and $\lambda = 1.00$ and $\lambda = 0.05$. Runs were performed for $\lambda = 1, 0.95, 0.9, 0.8, 0.5, 0.25$, and 0.05 and for different values of β. The results were not sensitive to the particular value of β used. The results changed uniformly with λ; hence the curves for $\lambda = 1.00$ and $\lambda = 0.05$ represent the extreme curves found.

For $\lambda = 0.05$, more is harvested at lower population sizes, while less is harvested at larger population sizes.

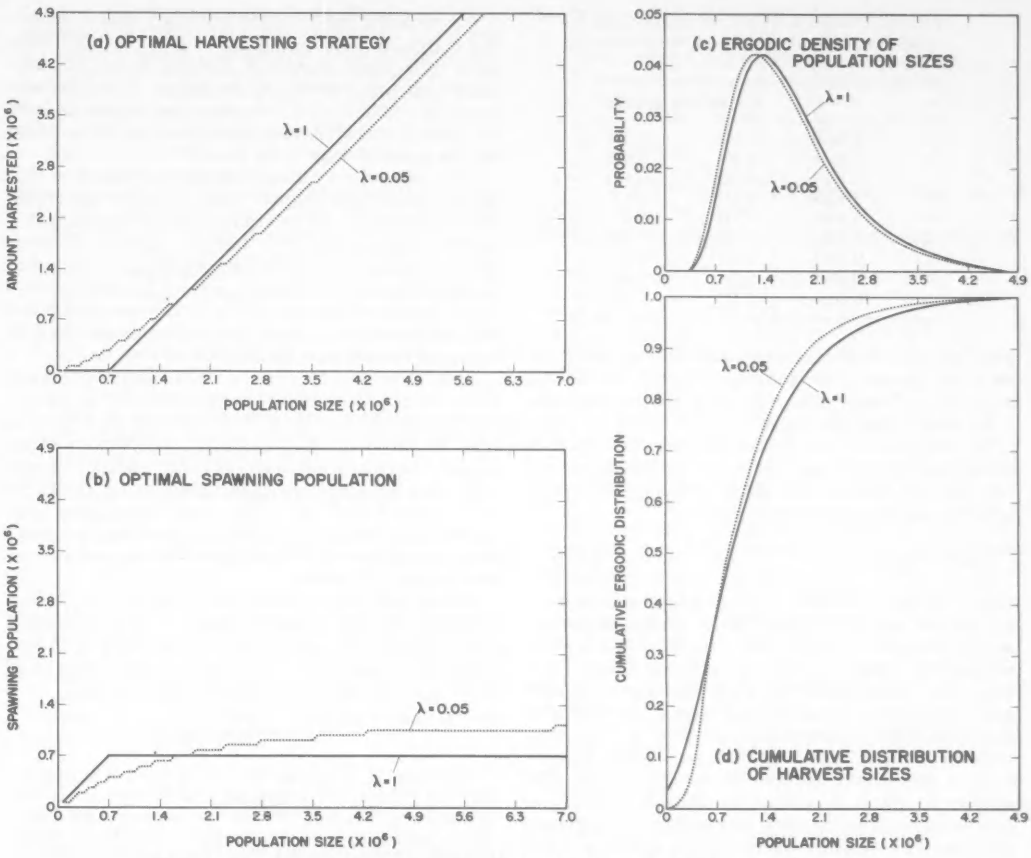

FIG. 3. Effects on an optimal policy and optimal value from varying the degree of risk aversion.

The crossover point is at a population size of 1.89×10^6, which is where (letting $\bar{d}$ denote the mean of d) the equation $\bar{d}4.082y \exp\{-0.8y\}$ has a value equal to $y = 1.89 \times 10^6$. Thus at the crossover point an individual just replaces itself in expectation.

Unlike the case for changes in β, the cumulative harvest distributions when λ varies differ by as much as 8%, and at the most probable harvest sizes, by about 5−6%. These differences are small but significant; the smaller values of λ can be seen to produce a "smoother" harvest in the long run.

These results can best be explained by considering the economic interpretation of the utility functions. At $\lambda = 1$, the price does not vary with supply (in fact it is $p = 1$, which can be viewed as the normalized price); therefore a harvest policy is based entirely on being as close as possible to the point of largest overall expected growth. However, at $\lambda = 0.05$, at low populations, the higher price (i.e. the higher risk) makes it desirable to harvest some now (i.e. the risk makes it desirable to obtain some amount of certain return now). At higher population levels, a balance must be maintained between a desirable price and future growth. For $y \geq 1.89 \times 10^6$, the expected value of x_{t+1} is less than y_t. Harvesting more now lowers the present marginal price per unit of fish, but increases the probability (i.e. decreases the risk) of larger population sizes next period (i.e. of small, unprofitable harvests next period).

The problem of unsmooth harvests from random populations is discussed in Mendelssohn (1976, 1980a, 1980b), Beddington and May (1977), and May et al. (1978). These empirical results suggest that unsmooth harvests have been found in the past because no effort has been made to include in management policies either attitudes towards risk, or marginal prices that are sensitive to supply. A reasonable conjecture is that all other things being equal, for a properly managed random fishery, wider fluctuations in catch will be expected either if outside supplies affect prices or if the entire quota cannot be taken by the fleet. Conversely, smaller fluctuations will be expected when the marginal price is very sensitive to the supply of the managed stock of fish only. Inventories can be viewed as an outside supply that affects

TABLE 1. Changes in relative risk aversion with changes in planning horizon length when following an optimal policy.

n	$\lambda = 1$	$\lambda = 0.5$	$\lambda = 0.05$
2	0.1430	0.0518	0.045
3	0.1684	0.303	0.423
4	0.1684	0.325	0.423
5	0.1684	0.331	0.423
6	0.1684	0.331	0.423
7	0.1684	0.331	0.423
8	0.1684	0.331	0.423
9	0.1684	0.331	0.423
10	0.1684	0.331	0.423

price, and they should have a very destablilizing effect if not taken into account in setting management policy for biologically random fisheries. This is precisely what has been seen in the salmon fishery in Alaska.

The solution of Eq. (2) offers some insights into relative risk aversion and planning horizons when optimal policies are followed. This is because Eq. (2) can be solved by solving the following sequence of recursive equations:

$$f_n(x) = \max_{0<y<x} g(x, y) + \beta E f_{n-1}(s[y, d])$$

where n denotes the number of periods remaining in the planning horizon. For Eq. (2), each $f_n(\bullet)$ is concave and continuous (Mendelssohn and Sobel 1980), and hence each is a risk averse utility. Each $f_n(x)$ is the utility of having x units of fish when there are n periods left when following *an optimal policy*. Hence $f_n'(x)$ is the marginal value of one additional unit of fish with n periods remaining, and the two risk averse measures R_1 and R_2 can be calculated as n changes (derivatives are approximated by finite differences) (Table 1). The measure R_2 reflects the relative risk aversion faced by the decision maker given the actual sample paths that will occur when following an optimal policy. What is noticeable is that the relative risk for f_n is much less than that for v_2, that it increases with n, and that it quickly becomes stationary after three to five periods. An optimal harvesting policy reduces the relative risk of the decision maker. Moreover, the effective planning horizon for these problems appears to be 3–5 yr, after which both policy, risk, and preferences remain stationary.

The measure of relative risk R_2 can be seen to be almost a measure of elasticity of the present marginal value of a unit of fish. As an optimal policy "smooths out" the supply of fish, the elasticity of the value per unit of fish decreases.

Conclusions

Any conclusions to be drawn from these results must be tempered by the realization that the results are derived from only limited numerical experimentation. However, the appendix presents theoretical results which suggest that over a broad class of stochastic harvesting models large changes in the discount factor produce only very small changes in an optimal harvesting policy. Hence, there is reason to believe the numerical results are in fact robust.

The numerical results suggest that policy often is insensitive to changes in the discount factor over a range of values likely to be found in practice. Discount factors may adequately represent intertemporal preferences for a dollar now versus an expected dollar in the future, but they do not seem to capture the attitude towards the degree of gamble in obtaining that expected dollar in the future.

Moreover, when the utility functions are viewed as total revenue curves with marginal price sensitive to supply, the results suggest that for optimally managed fisheries highly supply-sensitive prices will lead to stabilized harvests, whether the fishery is economically or biologically stochastic. As most if not all fisheries are stochastic, the usual assumption of perfect competition in fishery economic models and the lack of attention to risk preferences limit the usefulness of the results derived from these models.

External decisions for a fishery, such as entry decisions and enhancement projects, depend on the valuation of the fishery. The valuation of the fishery depends on the utility function used, the discount factor used, and the sample paths of the random harvest stream. Usually, the fishery manager can only control this last aspect through harvesting policy. The results of this paper suggest that under optimal management, misspecification of the discount factor in determining the optimal harvesting policy will have little effect on the external decisions of other parties.

Finally, as the degree of risk aversion increases, the amount harvested is not strictly nondecreasing for all population sizes. This seemingly is in contradiction with the results of Cropper (1976). The numerical results yield an intuitive explanation of why Cropper's result is not correct for this problem.

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ANDERSON, L. G. 1977. The economics of fisheries management. Johns Hopkins University Press, Baltimore. 214 p.

BEDDINGTON, J. R., AND R. M. MAY. 1977. Harvesting natural populations in a randomly fluctuation environment. Science (Washington, D.C.) 197: 463–465.

CLARK, C. W. 1976. Mathematical bioeconomics: the optimal management of renewable resources. John Wiley & Sons, New York. 352 p.

1980. Towards a predictive model for the economic regulation of commercial fisheries. Can. J. Fish. Aquat. Sci. 37: 1111–1129.

CROPPER, M. 1976. Regulating activities with catastrophic environmental effects. J. Econ. Environ. Manage. 3: 1–15.

HILBORN, R., AND C. J. WALTERS. 1977. Differing goals of salmon management on the Skeena River. J. Fish. Res. Board Can. 34: 64–72.

HOLLING, C. S. [ed.] 1978. Adaptive environment assessment and management. John Wiley & Sons, New York. 377 p.

KEENEY, R. L. 1977. A utility function for examining policy affecting salmon on the Skeena River. J. Fish. Res. Board Can. 34: 49–63.

KEENEY, R. L., AND H. RAIFFA. 1976. Decisions with multiple objec-

tives. John Wiley & Sons, New York. 596 p.

MATHEWS, S. B. 1967. The economic consequences of forecasting sockeye salmon runs to Bristol Bay, Alaska: a computer simulation study of the potential benefits to a salmon canning industry from accurate forecasts of the runs. Ph.D. dissertation, University of Washington, Seattle.

MAY, R. M., J. R. BEDDINGTON, J. W. HORWOOD, AND J. G. SHEPARD. 1978. Exploiting natural populations in an uncertain world. Math. Biosci. 42: 219–252.

MENDELSSOHN, R. 1976. Harvesting with smoothing costs. SWFC Admin. Rep. 9H, 1976, 20 p. SWFC Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.

1978. Determining the best trade-off between expected economic return and the risk of undesirable events when managing a randomly varying population. J. Fish. Res. Board Can. 36: 939–947.

1980a. A systematic approach to determining mean-variance tradeoffs when managing randomly varying populations. Math. Biosci. 50: 75–84.

1980b. Using Markov decision models and related techniques for purposes other than simple optimization: analyzing the consequences of policy alternatives on the management of salmon runs. Fish. Bull. U.S. 78: 35–50.

MENDELSSOHN, R., AND M. J. SOBEL. 1980. Capital accumulation and the optimization of renewable resource models. J. Econ. Theory 23: 243–260.

MERTON, R. C. 1969. Lifetime portfolio selection under uncertainty: the continuous time case. Rev. Econ. Statist. L1: 247–257.

1971. Optimal consumption and portfolio rules in a continuous time model. J. Econ. Theory 3: 373–413.

REED, W. J. 1974. A stochastic model for the economic management of a renewable animal resource. Math. Biosci. 22: 313–337.

WALTERS, C. J. 1975. Optimal harvest strategies for salmon in relation to environmental variability and uncertain production parameters. J. Fish. Res. Board Can. 32: 1777–1784.

WALTERS, C. J., AND R. HILBORN. 1976. Adaptive control of fishing systems. J. Fish. Res. Board Can. 33: 145–159.

Appendix

This appendix presents a rationale, but not a total proof, of why in a general setting policy, will change only slightly with changes in the discount factor. The notation and discussion follow Mendelssohn and Sobel (1980). The dynamic programming formulation of the optimal harvesting problem is

$$f(x) = \max_{x \in Y(x)} \{G(x, A(x)) + \beta E f(s[A(x), d])\}$$

For convenience, assume that an optimum always occurs at an interior point, which is true for one-period reward functions like $\ln(x - y)$. Then the optimality conditions are

$$G^{[2]}(x, A(x)) + \beta E f'(s[A(x), d]) s^{[1]}[A(x), d] = 0$$

By substitution, this yields

$$G^{[2]}(x, A(x)) + \beta E G^{[1]}(s[A(x), d], A(s[A(x), d])) s^{[1]}(A(x), d) = 0$$

For the specific case of $G(x, y) = (x - y)^{\lambda}$, this reduces to

$$\lambda(x - A(x))^{\lambda - 1} + \beta E\{\lambda(s[A(x), d] - A(s[A(x), d]))^{\lambda - 1} s^{[1]}[A(x), d]\} = 0$$

or that

$$E\{\lambda(s[A(x), d] - A(s[A(x), d]))^{\lambda - 1} s^{[1]}[A(x), d]\} = \frac{\lambda(x - A(x))^{\lambda - 1}}{\beta}$$

Suppose the discount factor is perturbed to $\beta + \delta$, such that $0 \leq \beta + \delta < 1$. Then at the value $A(x)$, the derivative has changed value by an amount

$$\frac{\delta\lambda(x - A(x))^{\lambda - 1}}{\beta}$$

Let $\gamma = |\lambda - 1|$, then this is equivalent to

$$\frac{\delta\lambda}{\beta(x - A(x))^{\gamma}}$$

For example, for $\beta = 0.9$, $\lambda = 0.5$, and $\delta = -0.2$ (so that the new discount factor is 0.7), the resulting term is

$$\frac{-0.0111}{(x - A(x))^{1/2}}$$

so that the derivative is still almost zero at $A(x)$. Moreover, $s[\bullet, d]$ is concave, and an optimum is most often at values of y where $s^{[1]}[\bullet, d]$ changes rapidly. Hence, it requires very small changes in an optimal policy to account for even relatively large changes in the discount factor.

Analysis of Longitudinal Zonation and the River Continuum Concept in the Oldman–South Saskatchewan River System

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CULP, J. M., AND R. W. DAVIES. 1982. Analysis of longitudinal zonation and the river continuum concept in the Oldman–South Saskatchewan River system. Can. J. Fish. Aquat. Sci. 39: 1258–1266.

During the summer–fall periods, the benthic macroinvertebrate communities of the Oldman–South Saskatchewan River system demonstrated a longitudinal zonation related to the subalpine forest, fescue prairie, and mixed prairie terrestrial ecosystems through which it flows. This zonation was primarily attributable to significant downstream increases in periphyton biomass, plant nutrients, and water temperature. Zonation was reduced in the late winter–spring periods and absent in May, during spring runoff. Longitudinal trends in macroinvertebrate functional feeding groups generally followed the predictions of the river continuum concept, with trophic composition apparently more strongly affected by autotrophic processes in the summer, and heterotrophic processes in the winter. By combining the river continuum concept with a watershed classification system based on geology, climate, soil type, and terrestrial vegetation, we suggest that biological comparisons of longitudinal zonation are enhanced.

Key words: longitudinal zonation, reciprocal average ordination, river continuum concept, functional groups

CULP, J. M., AND R. W. DAVIES. 1982. Analysis of longitudinal zonation and the river continuum concept in the Oldman–South Saskatchewan River system. Can. J. Fish. Aquat. Sci. 39: 1258–1266.

En été et en automne, les communautés de macroinvertébrés benthiques dans le réseau des rivières Oldman–Saskatchewan sud exhibent une zonation longitudinale reliée aux écosystèmes terrestres de forêt subalpine, de prairie de fescue et de prairie mixte qu'elles traversent. Cette zonation est attribuable en grande partie à d'importantes augmentations en aval de biomasse périphytonique, de nutriments végétaux et de température de l'eau. Elle est moins prononcée à la fin de l'hiver et au printemps, et absente en mai, au moment des crues printannières. Chez des groupes alimentaires fonctionnels de macroinvertébrés, les tendances longitudinales s'accordent en général avec les prédictions du concept de continuum fluvial, la composition trophique étant apparemment influencée à un plus haut degré par des processus autotrophes en été et des processus hétérotrophes en hiver. Nous suggérons qu'une combinaison du concept de continuum fluvial et d'un système de classification des bassins hydrographiques fondé sur la géologie, le climat, le type de sol et la végétation terrestre revaloriserait les comparaisons biologiques de la zonation longitudinale.

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LOTIC macroinvertebrate communities consist of intergrading populations whose structure and function reflect the underlying biotic and abiotic environments (Vannote et al. 1980). These communities are presumed to exhibit zones of faunal similarity, but to date no classification system has been widely accepted (Hynes 1970; Hawkes 1974). Rather than attempting to develop a universal system for the classification of macroinvertebrate communities, we feel it is more important to determine if, and when, zonation of macroinvertebrate communities and biological processes occurs, and which factors primarily affect zonation. Multivariate analysis, such as cluster analysis (Green and Vascotto 1978), or reciprocal averaging ordination (Culp and Davies 1980) can be used to examine zonation as both analyses identify groups of sites with similar community structure and composition.

This study is the first detailed investigation of the composition and structure of the Oldman and South Saskatchewan River macroinvertebrate communities. The analysis is designed to determine (1) if the fauna of these rivers could be divided longitudinally into zones of similar composition; (2) whether the zones changed seasonally; (3) if the observed zonation was related to the longitudinal trends of the measured environmental variables; and (4) if the macroinvertebrate communities were distributed as predicted by the river

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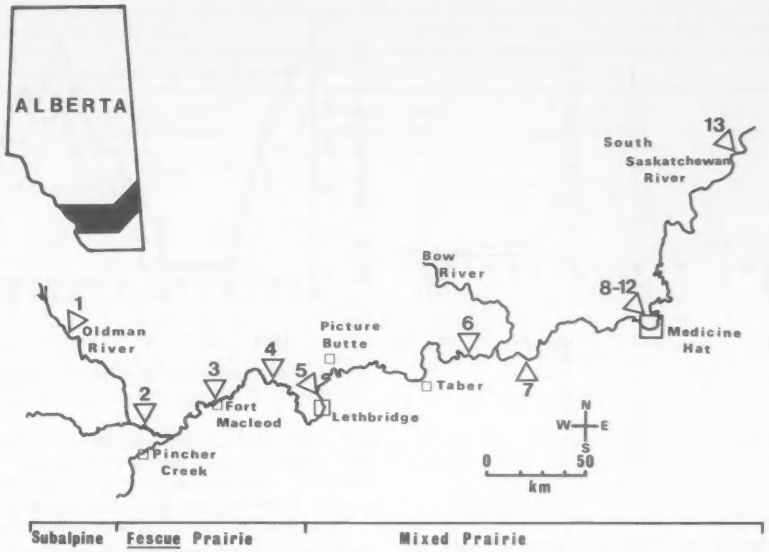

FIG. 1. Location of the sampling sites on the Oldman (sites 1–6) and South Saskatchewan (sites 7–13) rivers. The three terrestrial vegetation zones through which the rivers flow are indicated.

TABLE 1. Elevation, mean gradient, stream order (sensu Strahler 1957), and surrounding vegetation of the 13 sampling sites on the Oldman (1–6) and South Saskatchewan (7–13) rivers.

Sampling sites	Elevation range (m)	Mean gradient (m/km)	Stream order	Surrounding vegetation
1	1525–1065	5.75	3	Subalpine forest
2–4	945–885	1.33	4–5	Fescue prairie
5–6	840–775	1.20	5	Mixed prairie
7–13	700–610	0.36	6	Mixed prairie

continuum concept (Vannote et al. 1980).

Study Area

The South Saskatchewan River Basin in southern Alberta traverses three terrestrial vegetation zones: subalpine forest (Rowe 1972), fescue prairie, and mixed prairie (Coupland 1961). Thirteen sites were sampled along the river system (Fig. 1) with at least one sampling site in each vegetation zone (Table 1). Although much of the 38–46 cm/yr of precipitation received by the catchment falls during the ice-free period (April–November), peaks in discharge and suspended sediments usually result from spring runoff and summer spates (Fig. 2a and b). Water temperatures progressively increase downstream during the ice-free period with maximum temperatures of about 22°C occurring in July at site 5 (Fig. 3). Oxygen saturation was never less than 90%. The effluent from five sewage treatment plants enter the Oldman and South Saskatchewan rivers at Lethbridge, Picture Butte, Taber, and Medicine Hat, and to the Bow River below Calgary.

Methods

Macroinvertebrate samples were collected on 10 dates between August 1975 and March 1977 with 9–12 sites sampled during the ice-free period, and 5 sites in March 1976 and 1977. Three replicates per site were taken with a modified Neil (1938) cylinder, with 250-μm mesh netting, from substrate composed of gravel (2–64 mm) and rubble (64–160 mm), at a water depth of 40–60 cm. Detritus and all invertebrates were separated from the inorganic substrate in the field by swirling the sample in a pail of water, and repeatedly decanting the suspended organic material into a 125-μm mesh sieve before preservation in 80% ethanol. After the removal of invertebrates, the detritus was split into coarse (CPOM) and fine (FPOM) particulate organic matter, and the ash-free dry weight (375°C) determined. Periphyton biomass was estimated each samping period from three replicate 2.54-cm^2 scrapings according to the methods outlined in Green and Davies (1980). Methods for sampling the physical–chemical variables (Table 2) are presented in (Davies et al. 1978). We used the Mann–Whitney U-test (Sokal and Rohlf 1969) to establish significant differences in the physical–chemical variables, CPOM, and periphyton biomass between zones.

Data matrices for the macroinvertebrate collections were reduced in size to facilitate computer analysis by eliminating all taxa comprising less than 1% of the total number of individuals in a sample. Although this criterion reduced taxa numbers during periods of high and low species richness, from 77 to 52 in September 1975, and from 53 to 23 in March 1976, less than 5% of the total numbers of any sample was eliminated; no effects on functional group ratios resulted.

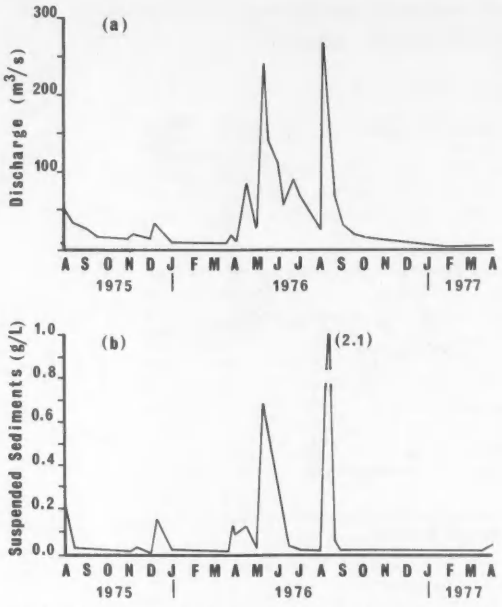

FIG. 2. (a) Mean monthly discharge (m^3/s) (based on daily means). (b) Mean daily suspended sediments (g/L) (based on daily means) at site 2. Trends of discharge and suspended sediments at site 2 are similar to all other sampling sites.

Reciprocal averaging (RA) ordination was utilized to produce two-axis ordinations of sites and species for each month (Culp and Davies 1980). Centroid values and confidence regions for each site were calculated from the replicate samples using the equations of Sokal and Rohlf (1969) to aid in the determination of site-groupings. Because of the high variability expected between replicate samples (Gauch and Whittaker 1972), we chose 80% confidence intervals.

Results

SITE ANALYSIS

The data for each month from the sites sampled were analyzed using RA ordination (Fig. 4). The RA analysis for March 1976 and 1977 were very similar and only the former is illustrated.

Ordination of the August 1975 sampling sites (Fig. 4a) showed no overlap between the 80% confidence region of site 1 (zone I) and the downstream sites. The eight remaining sites formed two groups, each with similar faunal compositions: sites 2, 3, and 4 of the upper Oldman River (zone II), and sites 6, 8, 9, 11, and 12 of the lower Oldman and South Saskatchewan rivers (zone III). The division between the two groups was not distinct because the confidence regions of sites 2 and 4 overlapped with sites in the other group.

RA ordinations of the summer–fall periods of August to October 1975, and July to September 1976 (Fig. 4a, b, c, h, and i), delimited a longitudinal pattern similar to the three-zone categorization of August 1975, although in September and October 1975, when site 1 was not sampled, only the sites in zones II and III were delineated (Fig. 4b and c).

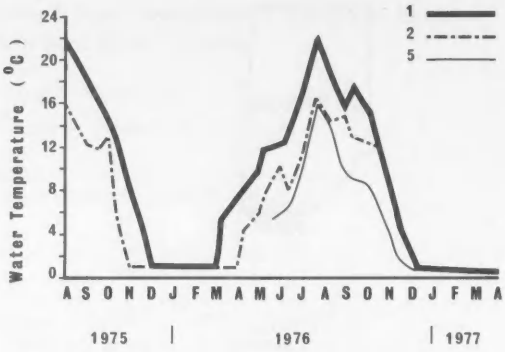

FIG. 3. Mean monthly maximum water temperatures (based on weekly means) at sites 1, 2, and 5.

The longitudinal pattern of the macroinvertebrate communities evident in the summer–fall was largely absent during the late winter–spring period (March–May 1976) (Fig. 4d, e, and f). Despite the absence of any distinct longitudinal pattern, the Oldman River sites were more similar to each other than to the South Saskatchewan River sites in March 1976 and 1977 (Fig. 4d). The confidence region of site 8 did not overlap with any sampling sites in May 1976 (Fig. 4f), and in April 1976 (Fig. 4e), the macroinvertebrate community of site 1 was delimited from the downstream sites.

The June 1976 benthic communities (Fig. 4g) revealed site-groupings transitional between those of the late winter–spring and summer–fall periods. Sites 1 and 2 of the Oldman River were delimited from the other sites and were more similar to sites 3 and 4 than the other sites. The 80% confidence regions of sites 3–12 overlapped.

TAXONOMIC ANALYSIS

Table 3 lists the taxa that had mean seasonal abundances greater than 5% during at least one season. The 61 taxa with seasonal abundances <5% were omitted from Table 3 but are listed in Appendix 1. Table 4 indicates the number of all taxa unique to, or shared between, the zones. Many invertebrate groups could not be identified to species because of the lack of adequate taxonomic keys. This problem may affect the analysis by masking longitudinal zonation of congeneric species or confamilial genera (e.g. Chironomidae).

The summer–fall 1975 macroinvertebrate fauna of zones I and II were dominated by Ephemeroptera taxa (Fig. 5a), although the dominant genera differed between the zones (Table 3). *Pericoma*, *Rhyacophila*, and *Ephemerella coloradensis* were the only taxa unique to zone I. Eighteen taxa were unique to zone II (Table 4), but the more abundant taxa in zone II had distributions that overlapped with one or both of the adjacent zones (Table 3). The fauna of zone III was distinct from the upstream zones (Fig. 5a) because of

TABLE 2. The seasonal means for environmental variables of the Oldman and South Saskatchewan rivers which showed a significant zonal difference during at least one season. Total alkalinity and hardness are expressed as mg $CaCO_3$/L; conductivity in μS/cm at 20°C; SiO_2, total and dissolved phosphorus, nitrates, total and dissolved nitrogen, particulate organic carbon, and suspended sediments in mg/L; periphyton biomass in mg/cm, and coarse particulate organic matter (CPOM) in mg/m^2. (* = $P < 0.05$, ** = $P < 0.01$.)

	Summer–fall 1975 vegetational zone			Late winter–spring vegetational zone			June 1976 vegetational zone			Summer–fall 1976 vegetational zone		
	I	II	III	I	II	III	I	II	III	I	II	III
Total alkalinity	—	160*	130*	—	150	145	—	105	115	—	145*	125*
Conductivity	250	290*	272*	180	294	287	170	190	237	193	216	235
Total hardness	—	187*	150*	—	240	237	—	120	133	—	153*	117*
Nitrates	—	0.01*	0.14*	—	0.08*	0.39*	—	0.02	0.01	—	0.03	0.04
Total nitrogen	—	0.14*	51*	—	1.65	1.39	—	0.72	2.22	—	0.75*	1.33*
Dissolved nitrogen	—	0.11*	0.30*	—	0.45	0.77	—	0.10	0.48	—	0.13	0.15
Total phosphorus	—	0.008*	0.033*	—	0.014*	0.019*	—	0.081	0.089	—	0.041	0.057
Dissolved phosphorus	—	0.005*	0.015*	—	0.004*	0.048*	—	0.010	0.008	—	0.003*	0.015*
SiO_2	—	3.9*	0.5*	—	5.2*	2.8*	—	4.9*	2.5	—	4.6*	2.0*
Suspended sediments	—	15	34	19	71*	221*	7	21*	57*	93	134*	232*
Particulate organic carbon	—	—	—	—	—	—	—	0.73	1.40	—	0.31*	1.00*
Periphyton biomass	0.08*	2.03**	6.00**	0.01	0.31**	3.19**	0.1	0.45	0.29	—	0.18**	1.85**
CPOM	—	—	—	10	18	13	9	17*	4*	7	6	—

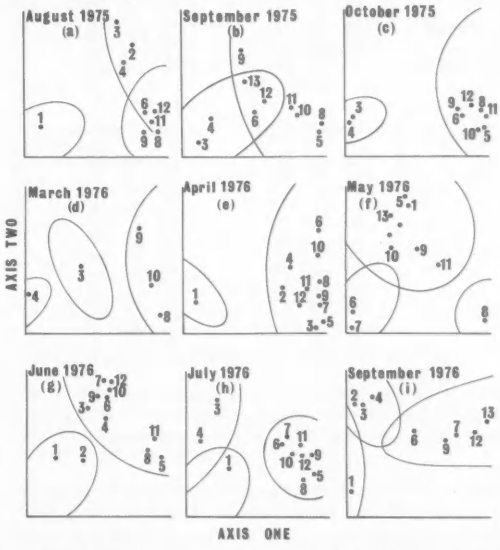

FIG. 4. Reciprocal averaging of all sites sampled in (a) August 1975, (b) September 1975, (c) October 1975, (d) March 1976, (e) April 1976, (f) May 1976, (g) June 1976, (h) July 1976, and (i) September 1976. Eighty percent confidence region borders shown.

large increases of Chironominae and *Tricorythodes*, a reduction in the number of *Baetis* and *Rhithrogena*, and the 18 unique taxa (Tables 3 and 4). Five taxa (Orthocladiinae, Tanypodinae, Oligochaeta, *Baetis*, and *Rhithrogena*) were shared between zones I, II, and III.

The late winter–spring composition of zone I was again numerically dominated by the Ephemeroptera genera *Baetis* and *Rhithrogena* (Table 3; Fig. 5b). During this period the fauna of zones II and III were dissimilar to zone I, and were dominated by Orthocladiinae and Chironominae (Table 3; Fig. 5b). Of the numerous unique taxa collected from zones II and III, only *Ephemera simulans* and *Ephoron album* of zone III had an abundance >5% (Table 3).

The June 1976 fauna of zones I, II, and III were dominated by Ephemeroptera, followed by Chironomidae, and Plecoptera (Fig. 5c). All three zones were distinct with many zone-restricted taxa (Table 4). Community composition in zone I exhibits a seasonal shift to greater number of Chironomidae and a decrease in Plecoptera. Zones II and III show greatly decreased numbers of Chironomidae and increases in Ephemeroptera.

The summer–fall 1976 fauna of zones I, II, and III (Fig. 5d) were similar to those of June 1976 (Fig. 5c), except for the increase in numbers of Trichoptera in all three zones, and increased numbers of Plecoptera in zone I. This similarity at the ordinal and familial level masks the clear longitudinal distinctions between the zones as unique taxa were present in each zone (Table 4): 12 taxa in zone I; 14 in zone II; and 18 in zone III. Compared to the summer–fall period of 1975, the fauna of zones I and II were similar, although in 1976 the Chironomidae increased, and the Trichoptera and Ephemeroptera decreased. The zone III fauna differed from that of summer–fall 1975 primarily because of lower percentages of the Chironomidae and Trichoptera, and the large increase in Ephemeroptera in summer–fall 1976 (Fig. 5a and d).

TROPHIC GUILD ANALYSES

Figure 6a, b, c, and d illustrate the trophic guild composition of zones I–III for the four seasonal periods using the functional group classification of Merritt and Cummins (1978), and Hawkins and Sedell (1981) (Table 3, Appendix 1).

The collector–scraper category was the dominant trophic guild during every seasonal period at zone I, whereas its

TABLE 3. Mean seasonal abundance and trophic guild category of the macroinvertebrate taxa of the Oldman and South Saskatchewan rivers. Sixty-one taxa with seasonal abundance never greater than 5% are listed in Appendix 1 (r = 1−5%, f = 5−25%; c > 25−50%; a > 50−75%) (C = collector, G = gatherer, Sc = scraper, F = filterer, Shr = shredder, E = engulfer).

		Zone I				Zone II				Zone III			
				1976				1976				1976	
Taxa	Trophic guild	1975 Summer–fall	Late winter–spring	June	Summer–fall	1975 Summer–fall	Late winter–spring	June	Summer–fall	1975 Summer–fall	Late winter–spring	June	Summer–fall
Epeorus (Ironopsis)	C–Sc		*r*		*f*								
Pericoma	C–G	*r*	*f*	*r*	*r*								
Rhyacophila	C–G	*f*	*r*	*r*	*r*								
Cinygmula	C–Sc		*r*	*f*	*f*			*f*	*r*				
Zapada	Shr	*r*	*r*	*f*	*r*	*r*							
Isonychia	C–F	*f*	*r*		*f*	*r*	*r*	*r*					
Ephemerella coloradensis	C–Sc	*f*			*r*			*r*	*r*				
Taenionema	C–Sc		*r*		*f*		*r*						
Tricorythodes	C–G					*r*	*r*	*r*	*r*	*c*	*r*	*r*	*c*
Cheumatopsyche	C–F					*f*	*r*	*r*	*r*	*f*	*f*	*r*	*f*
Heptagenia	C–Sc					*f*	*r*	*r*	*r*	*f*	*f*	*r*	*r*
Isoperla	E					*r*	*r*	*f*	*r*	*r*	*f*	*f*	*r*
Symphitopysche	C–F					*f*	*r*	*r*	*f*	*f*	*r*	*r*	*f*
Ephemerella inermis	C–Sc					*f*	*f*	*f*	*r*	*r*	*r*	*f*	*r*
Choroterpes	C–Sc					*r*			*r*	*f*	*r*		*r*
Ephemera simulans	C–G									*f*	*f*	*r*	*r*
Ephoron album	C–G									*f*			*f*
Baetisca										*r*	*f*	*r*	*r*
Orthocladiinae	C–G	*r*	*f*	*f*	*f*	*f*	*c*	*f*	*f*	*f*	*a*	*f*	*f*
Rhithrogena	C–Sc	*r*	*f*	*c*	*f*	*a*	*f*	*f*	*c*	*r*	*r*	*r*	*r*
Baetis	C–Sc	*f*	*f*	*f*	*f*	*f*	*r*	*f*	*f*	*r*	*f*	*c*	*f*
Chironominae	C–G		*r*		*r*	*r*	*f*	*r*	*f*	*c*	*f*	*f*	*f*
Tanypodinae	E	*r*	*r*	*r*	*r*	*r*	*r*	*r*	*r*	*f*	*r*	*f*	*r*

TABLE 4. The number of all taxa collected with distributions unique to, or overlapping between, the zones of the Oldman and South Saskatchewan rivers. Taxa comprising less than 1% in a sample were omitted.

Zonal distribution	1975		1976	
	Summer–fall	Late winter–spring	June	Summer–fall
Zone I	3	14	6	12
Zone II	18	16	17	14
Zone III	18	13	9	18
Zones I and II	2	8	4	8
Zones II and III	8	8	7	8
Zones I–III	5	6	5	6

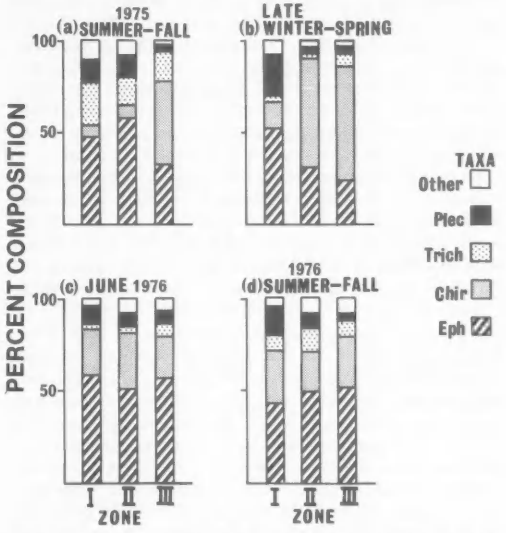

FIG. 5. Percentage composition of the Ephemeroptera (Eph), Chironomidae (Chir), Trichoptera (Trich), and Plecoptera (Plec) in faunal zones I–III during (a) summer–fall 1975, (b) late winter–spring, (c) June 1976, and (d) summer–fall 1976.

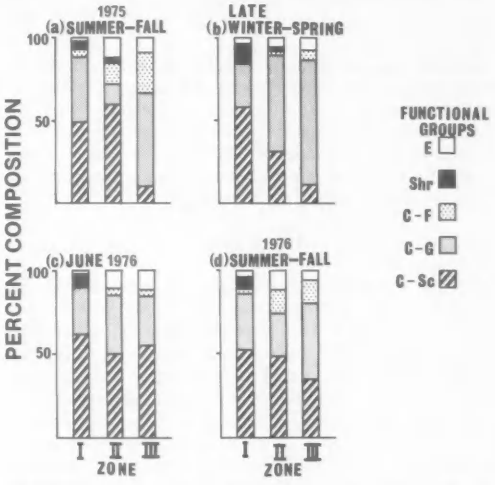

FIG. 6. Percentage composition of the functional feeding groups in faunal zones I–III during (a) summer–fall 1975, (b) late winter–spring, (c) June 1976, and (d) summer–fall 1976. Piercer abundance never exceeded 2% and have been omitted. (E = engulfer, Shr = shredder, C–F = collector–filterer, C–G = collector–gatherer, C–Sc = collector–scraper).

percentage dominance was restricted to the summer–fall and June periods in zone II, and to June in zone III (Fig. 6). A sharp longitudinal decrease in this trophic component occurred between zones II and III in the summer–fall (Fig. 6a and d) and late winter–spring (Fig. 6b), and between zones I and II in the late winter–spring (Fig. 6b).

The collector–gatherer guild was not dominant in zone I, but always remained a relatively constant and abundant trophic component. Collector–gatherer was the major component of zone III during the 1975-76 summer–fall periods (Fig. 6a and d). Increases in abundance of collector–gatherers were observed in the late winter–spring between zones I, II, and III, and formed the dominant category of zones II and III (Fig. 6b).

The shredder guild was most abundant in zone I in the late winter–spring and generally decreased in abundance from zone I to zone III in all seasons (Fig. 6). Conversely, the greatest percentages of the collector–filterer guild occurred in the summer–fall in zones II and III, and longitudinal increases were noted between zones I and III in most seasonal periods. Piercers (not illustrated) were also more abundant in zones II and III in the summer–fall, although their contribution never exceeded 2.0%.

Engulfers did not exhibit a distinguishable longitudinal trend, but their lowest percentage abundances always occurred in zone I, and zone II had the highest abundances in the summer–fall.

ANALYSIS OF ENVIRONMENTAL VARIABLES

Table 2 lists only the environmental variables that were significantly different between the zones, although current

velocity, pH, and oxygen saturation were also measured. Data for zone I could not be tested as a result of a lack of replication, but zone I always had the lowest conductivity and periphyton biomass values (Table 2). Suspended sediments increased sharply between zones I, II, and III, particularly during the spring runoff (May–June), and a 1-wk spate in August 1976 (Table 2; Fig. 2b).

Perhaps the most important difference between zones II and III (Table 2) was the higher periphyton biomass of zone III during the summer–fall and late winter–spring, which was associated with significantly lower concentrations of silica, and significantly higher concentrations of dissolved phosphorus. Zone III also had higher total phosphorus, total and dissolved nitrogen, and nitrates in summer–fall 1975, and higher particulate organic carbon (POC), suspended sediments, and total nitrogen in summer–fall 1976. Total phosphorus and nitrates were higher for zone III in late winter–spring.

CPOM values in zones II and III exhibited a downward trend from the late winter–spring; the largest amounts recorded in zone II in late winter–spring and June (Table 2). Estimates were not obtained for zone III in summer–fall 1976 because of the entrapment of CPOM by filamentous algae. Trends for FPOM were not evident because the presence of fine coal particles biased the estimates.

Discussion

During the summer–fall periods the macroinvertebrate communities of the Oldman and South Saskatchewan rivers were related to the three terrestrial botanical zones with distinct stream valley and channel features described by Kellerhals et al. 1972: zone I to the subalpine forest; zone II to the fescue prairie; and zone III to the mixed prairie. This relationship was partially attributable to enhanced algal biomass production related to the downstream increase in the availability of plant nutrients (e.g. dissolved nitrogen and phosphorus), particularly between zones II and III. Soil type and terrestrial nutrient cycling likely had a strong effect on the plant nutrient pool in each zone, but nutrient levels in zone III were additionally influenced by sewage effluents. The impact of nutrient additions to zone III is underscored by the lower diatom (Bacillariophyceae) biomass and dominance of the periphyton community of zone III by green algae (Chlorophyta) compared to zones I and II. Filamentous green algae, *Cladophora glomerata* and *Oedogonium* spp., accounted for 80–90% of the biomass in zone III (Green and Davies 1980).

Longitudinal differences in the summer–fall macroinvertebrate communities are probably, at least in part, related to the available food base. Communities in zones I and II were dominated by collector–scrapers (e.g. *Rhithrogena* and *Ephemerella inermis*) which can directly utilize the algal biomass (Cummins 1974). Zone I also had a large collector–gatherer component which probably reflects the importance of fine particulate organic matter (FPOM) derived from allochthonous inputs and the processing of the algal biomass. Conversely, in the area of highest algal biomass (zone III), the collector–gatherer (e.g. Orthocladiinae, Chironomidae, *Ephoron album*, and *Ephemera simulans*) and collector–filterer (e.g. *Symphitopsyche* sp. and *Cheumatopsyche* sp.) trophic categories were dominant, suggesting that the main result of the increased algal biomass was to enhance the availability of FPOM. Even though the taxonomic composition of summer–fall communities in the three zones varied widely between years, the longitudinal trophic structure of the communities was very similar.

Underlying the longitudinal change in the macroinvertebrate food base is a pronounced downstream increase in water temperatures from March to October. Zones I and II on the upper Oldman River have similar temperature profiles, but species in zone III accrue a considerably greater number of degree days (Fig. 3c). In fact, the life cycles of five Ephemeroptera taxa of zone III are related to spring and summer temperature requirements (Lehmkuhl 1972). Vannote and Sweeney (1980) have shown that adult body size and fecundity are largely dependent on the thermal conditions during aquatic insect larval growth, and they suggest that the thermal regime can strongly effect distributional patterns within drainage systems. Because many taxa were restricted to zones I and II, and, with the exception of the ubiquitous taxa, no taxonomic overlap occurred between zones I and III, the longitudinal thermal regime appears to be an important factor affecting macroinvertebrate distribution of these rivers.

In the late winter–spring period, only the fauna of zone I remained longitudinally distinct. The relatively constant trophic structure of zone I throughout the year implies a seasonal similarity in the major components of the macroinvertebrate food base. However, the increased winter importance of shredders and the summer increases in filter feeders suggest a seasonal response to leaf litter and algal inputs. The late winter–spring communities of zones II and III were dominated by collector–gatherers probably indicating a highly elevated FPOM detrital pool in the winter. Winter algal biomass in zones II and III was significantly lower than summer levels (Green and Davies 1980); therefore, the decline of the summer–fall algal communities could be the source of an enlarged winter FPOM level in zones II and III. Although fall and spring thermal conditions may influence species distributions, water temperature does not appear to be a major factor affecting winter community composition as the conditions of zones I–III were almost identical (Fig. 3c).

Spates and their associated high suspended sediment load affected community composition differently depending on the season and faunal zone. Spring flooding from the annual mountain runoff produced the most pronounced effects by reducing periphyton biomass in all three zones and shifting the postflood communities of zones II and III to a collector–scraper dominated trophic structure. Unlike the spring flood, which catastrophically affected the late winter–spring communities of zones II and III, the summer spate had no apparent effect on macroinvertebrate community composition or trophic structure.

The longitudinal trends in functional feeding groups generally followed the predictions of the river continuum concept (Vannote et al. 1980) and likely indicate that CPOM was less important to downstream communities where FPOM and algal biomass were more important nutritive sources. However, these trends were not always consistent between seasons. Macroinvertebrate trophic composition in zones II and III appeared to be strongly affected by enrichment and auto-

trophic processes during the summer, and heterotrophic processes in the winter. Although the strict application of the river continuum concept does not apply to this prairie river system in all seasons, its general framework of longitudinal shifts in macroinvertebrate trophic composition provides a useful interpretive tool through which macroinvertebrate zonation may be analyzed.

An appropriate starting point for river zonation studies is Lotspeich's (1980) outline for watershed classification which utilizes geology, macro- and micro-climate, soil type, and terrestrial vegetation as hierarchical classification criteria. For example, in this study, longitudinal zonation of macroinvertebrates of the Oldman and South Saskatchewan rivers were related to differences in water temperature, geomorphic features, terrestrial vegetation, soil type, and plant nutrients. By coupling longitudinal zonation studies with Lotspeich's hierarchical system and the river continuum framework, the biological comparison of streams in different geographical regions could be enhanced, and the understanding of biological processes significantly aided.

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COUPLAND, R. T. 1961. A reconsideration of grassland classification in the Northern Great Plains of North America. J. Ecol. 49: 135–167.

CULP, J. M., AND R. W. DAVIES. 1980. Reciprocal averaging and polar ordination as techniques for analyzing lotic macroinvertebrate communities. Can. J. Fish. Aquat. Sci. 37: 1358–1364.

CUMMINS, K. W. 1974. Structure and function of stream ecosystems. BioScience 24: 631–641.

DAVIES, R. W., J. M. CULP, R. GREEN, M. O'CONNELL, G. SCOTT, AND C. ZIMMERMAN. 1977. River classification of the South Saskatchewan River Basin. Vol. I. Technical Report, Pollution Control Division. Alberta Environment. 201 p.

GAUCH, H. G. JR., AND R. H. WHITTAKER. 1972. Comparison of ordination, techniques. Ecology 53: 868–875.

GREEN, R. B., AND R. W. DAVIES. 1980. The epilithic algae of the Oldman–South Saskatchewan River system, Alberta, Canada. Nova Hedwigia 33: 261–278.

GREEN, R. H., AND G. L. VASCOTTO. 1978. A method for the analysis of environmental factors controlling patterns of species composition in aquatic communities. Water Res. 12: 583–590.

HAWKES, H. A. 1975. River zonation and classification. *In* B. A. Whitton [ed.] River Ecology. Univ. California Press, Berkeley and San Francisco, CA. p. 312–374.

HAWKINS, C. P., AND J. R. SEDELL. 1981. Longitudinal and seasonal changes in functional organization of macroinvertebrate communities in four Oregon streams. Ecology 62: 387–397.

HYNES, H. B. N. 1970. The ecology of running waters. Univ. Toronto Press, Toronto, Ont. 555 p.

KELLERHALS, R., C. R. NEIL, AND D. I. BRAY. 1972. Hydraulic and geomorphic characteristics of rivers in Alberta. Tech. Rep. 72-1, Alberta Cooperative Research Program in Highway and River Engineering. 156 p.

LEHMKUHL, D. M. 1972. Change in thermal regime as a cause of reduction of benthic fauna downstream of a reservoir. J. Fish. Res. Board Can. 29: 1329–1332.

LOTSPEICH, F. B. 1980. Watersheds as the basic ecosystem: this conceptual framework provides a basis for a natural classification system. Water Res. Bull. 16: 581–586.

MERRITT, R. W., AND K. W. CUMMINS. 1978. Aquatic insects of North America. Kendall/Hunt Publishing Company, Dubuque, IA. 441 p.

NEIL, R. M. 1938. The food and feeding of the brown trout (*Salmo trutta* L.) in relation to the organic environment. Trans. R. Soc. Edinburgh 59: 383–409.

ROWE, J. S. 1972. Forest regions of Canada. Canadian Forestry Service, Department of the Environment, Ottawa. 171 p.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. The principles and practice of statistics in biological research. W. H. Freeman and Company, San Francisco, CA. 776 p.

STRAHLER, A. N. 1957. Quantitative analysis of watershed geomorphology. Trans. Am. Geophys. Union 38: 913–920.

VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL, AND C. E. CUSHING. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37: 130–137.

VANNOTE, R. L., AND B. W. SWEENEY. 1980. Geographical analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. Am. Nat. 115: 667–695.

Appendix 1.

Zonal distribution and trophic guild of 61 taxa with mean seasonal abundances never greater than 5%. (C = collector, G = gatherer, Sc = scraper, F = filterer, E = engulfer, P = piercer).

Taxa	Trophic guild	Zone I	Zone II	Zone III
Calineuria	E	+		
Dicranota	E	+		
Dolichopeza	?	+		
Ephemerella doddsi	C–Sc	+		
E. (Serratella)	C–Sc	+		
Hydroporus rivalis	P	+		
Kogotus	E	+		
Neothremma	C–Sc	+		
Perlomyia	Shr	+		
Prosimulium	C–F	+		
Arctopsyche	C–F	+	+	
Capnia	Shr	+	+	
Ceratopogonidae	E	+	+	
Epeorus (Iron)	C–Sc	+	+	
Glossoma	C–Sc	+	+	
Hastaperla	?	+	+	
Megarcys	E	+	+	
Parapsyche	C–F	+	+	
Atherix	P		+	
Centroptilum	C–Sc		+	
Ceraclea	C–G		+	
Chloroperlinae	C–G		+	
Claassenia sabulosa	E		+	
Cultus	E		+	
Dubiraphia	C–G		+	
Empididae	E		+	
Ephemerella (Danella)	C–Sc		+	
E. (Drunella)	C–Sc		+	
E. flavilinea	C–Sc		+	
E. tibialis	C–Sc		+	
Hydroporus griseostriatus	P		+	

Appendix 1 (*Concluded*)

Taxa	Trophic guild	Zone I	Zone II	Zone III
Isogenoides	E		+	
Lepidostoma	Shr		+	
Leptophlebia	C−G		+	
Limnophila	E		+	
Liodessus affinis	?		+	
Paragnetina	E		+	
Paraleptophlebia	C−G		+	
Paraperla	?		+	
Pteronarcella badia	?		+	
Pteronarcys californica	Shr		+	
Simulium	C−F		+	
Siphlonurus	C−Sc		+	
Caenis	C−G		+	+
Hexatoma	C−G		+	+
Agraylea	P			+
Ameletus	C−G			+
Brachycercus	C−G			+
Cataclysta	Shr			+
Corixinae	P			+
Dactylobaetis warreni	?			+
Helicopsyche borealis	C−Sc			+
Hydroptila	P			+
Nectopsyche	?			+
Oecetis	?			+
Ophiogomphus	E			+
Pisidium	C−F			+
Stenonema	C−Sc			+
Sphaerium	C−F			+
Traverella albertana	C−F			+
Oligochaeta	C−G	+	+	+

A Method for Predicting Winter Oxygen Profiles in Ice-covered Ontario Lakes

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JACKSON, M. B., AND D. C. LASENBY. 1982. A method for predicting winter oxygen profiles in ice-covered Ontario lakes. Can. J. Fish. Aquat. Sci. 39: 1267 – 1272.

A simple method is presented for predicting oxygen profiles under ice cover in selected Ontario lakes. The oxygen loss rate within individual lake strata over winter can be predicted from the oxygen concentration in each stratum about 5 – 15 d after freeze-up (at the time of maximum volume-weighted oxygen concentration for the lake). Shield lakes and limestone-transition lakes are described by two distinct relationships; the rate of oxygen loss per unit oxygen concentration is greater in the limestone-transition lakes.

Key words: lake-oxygen concentration, limestone lakes, lake respiration, oxygen profile, lake depth, oxygenation/oxidation processes, ice cover, Shield lakes

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Le présent article contient une description d'une méthode simple pour prédire les profils d'oxygène sous une couverture de glace dans certains lacs de l'Ontario. Le taux de perte d'oxygène dans des couches individuelles des lacs en hiver peut être prédit à partir de la teneur en oxygène dans chaque couche, environ 5 – 15 jours après le gel (au moment du maximum de concentration d'oxygène pondérée par volume pour le lac). Deux relations distinctes peuvent servir à décrire les lacs du Bouclier et ceux de transition de pierre à chaux; le taux de perte d'oxygène par unité de concentration d'oxygène est plus grand dans les lacs du deuxième type.

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WINTER fish-kill in lakes due to oxygen depletion has long been of concern to fisheries biologists (Greenbank 1945; Woods 1961; Casselman and Harvey 1975; and others) but only recently have limnologists attempted to predict potentially lethal oxygen concentrations under ice cover. Welch (1974), working on arctic lakes, and Barica and Mathias (1979), working on small prairie lakes, found that if the volume-weighted oxygen concentration of the lake at freeze-up is known or assumed and if the whole-lake respiration rate can be estimated, then it is possible to forecast the change in volume-weighted oxygen concentration during ice cover. Welch (1974) estimated whole-lake respiration rates from a minimum of two early winter oxygen profiles. Barica and Mathias (1979) found that whole-lake respiration rates (expressed per unit area) could be predicted from mean depth and maximum depth consistent with the findings of Welch et al. (1976).

Each of the above oxygen models can be used to predict "average" whole-lake oxygen concentration over winter. However, this average oxygen index provides no information on the vertical oxygen concentration profile in a lake. Therefore, a method is presented for predicting oxygen concentration "with depth" in selected Ontario lakes under ice cover.

Materials and Methods

The study lakes were selected primarily to ensure low winter flushing rates (hence minimizing the effect of oxygen input) and measurable winter oxygen loss. Table 1 gives some limnological characteristics of the study lakes. Lake St. George (45°57′N, 79°26′W) is a small perched kettle lake occupying a depression in clay material, underlain by shale and limestone. Coon Lake (44°37′N, 78°12′W) and Big Cedar Lake (44°36′N, 78°10′W) are small ice scour lakes in a region of transitional geology dominated by Precambrian igneous rock of the Canadian Shield and scattered outcroppings of sedimentary limestone to the south (Jackson 1979).

Coon Lake was sampled weekly and Lake St. George and Big Cedar Lake were sampled every 2 wk from September 1977 to May 1978. Dissolved oxygen, temperature, conductivity, and seston were measured at 2-m intervals at the deepest part of each lake. Oxygen concentrations were determined in duplicate using the azide modification of the Winkler method (APHA 1965). Conductivity (temperature corrected to 25°C) and temperature were measured with a YSI model 33

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TABLE 1. Some morphometric, chemical, physical, and plankton characteristics of the study lakes, December 5, 1977, to April 19, 1978.

Lake	Area (ha)	Max. depth (m)	Mean depth (m)	Catchment area (ha)	Mean near-ice chloro *a* ($mg \cdot L^{-1}$)	Mean volume weighted: Spec. cond. ($\mu S \cdot cm^{-1}$)	Seston ($mg \cdot L^{-1}$)	Temp. (°C)	D.O. ($mg \cdot L^{-1}$)
St. George	10.3	16	5.6	132	1.05	390	0.68	3.2	3.9
Coon	53.1	18	4.0	239	1.27	132	0.84	3.4	4.4
Big Cedar	224	18	6.3	1245	0.52	195	0.42	3.0	8.5

meter and submersible probe. Seston concentration was determined by filtering a known volume of lake water through a GF/C 4.25-cm filter (1.2-μm retention) which had been previously ashed (2 h at 500°C), rinsed in distilled water, dried to a constant weight (24 h at 60°C), and weighed. After filtering with lake water, each filter was again dried to a constant weight at 60°C. The difference in filter weight before and after filtering (including correction for weight change in three control filters run with distilled water) is seston dry weight. Volume-weighted expressions of each of the measured characters (Table 1) were obtained by multiplying the measured profile values by the volume of the corresponding strata, summing the results, and dividing by the lake volume. Snow and ice measurements were recorded in the immediate vicinity of each sampling station.

Results and Discussion

Model Development

The study lakes sustained permanent ice cover by late November to early December. Peak ice occurred in late March to early April and breakup was complete by May 1. In each lake, wind-induced oxygenation ceased with ice formation. Oxygen concentrations near the ice cover continued to increase in early winter, probably as a result of the combined effects of oxygen freeze-out during black ice formation and primary production. In contrast, oxygen concentrations near the sediments began to decrease immediately with the onset of ice cover as a result of sediment and water oxygen demand (Jackson 1979). The outcome of these two opposing phenomena is that the study lakes did not obtain maximum volume-weighted oxygen concentrations until about 5–15 d after ice formation.

In each of the study lakes, oxygen loss rates were determined for individual 2-m strata (Fig. 1). Rates increased nearer the sediments, possibly indicative of higher concentrations of oxidizable material (due to incomplete fall mixing) and/or the greater sediment surface area to water volume ratio at these increased depths (Rudd and Hamilton 1978; Jackson 1979). For the majority of strata, oxygen loss rates decreased with time, a semi-log relationship providing the best fit to the observed data.

$$(1) \quad [O_2] = b \cdot 10^{-k \cdot n}$$

where $[O_2]$ is the stratum-oxygen concentration (mg $O_2 \cdot L^{-1}$), k is the slope or stratum-oxygen loss rate (log mg $O_2 \cdot L^{-1} \cdot d^{-1}$), n is the day number (d), and b is the y intercept (mg $O_2 \cdot L^{-1}$).

Simple regression analysis was used to examine the relationships between k, as the dependent variable, and selected morphological, physical, and chemical characteristics of each stratum (Table 2). The limestone-transition study lakes showed a significant negative curvilinear relationship between k and $[O_2]_m$, stratum-oxygen concentration (mg $O_2 \cdot L^{-1}$) measured 5–15 d after freeze-up (at the time of maximum volume-weighted oxygen concentration for the lake) (Fig. 2).

$$(2) \quad k = 6.705 \cdot 10^{-0.2763[O_2]_m} \; (R = 0.94, P < 0.01)$$

The correlation coefficient was not noticeably improved by incorporating the effects of the other measured variables in stepwise multiple regression analysis (Table 3). Although seston concentration, $[S]_m$, was significantly correlated with k in simple regression analysis, $[S]_m$ was not significant in the multiple regression procedure because of its strong intercorrelation with $[O_2]_m$.

The relationship between k and $[O_2]_m$ was also determined for a number of Ontario Shield lakes which included Red Chalk Lake, located in the district of Haliburton (Ontario Ministry of the Environment, unpublished data), and four northwestern Ontario lakes (Schindler 1971). Again the relationship was negative and significant.

$$(3) \quad k = 0.198 \cdot 10^{-0.2165[O_2]_m} \; (R = 0.74, P < 0.01)$$

Figure 2 illustrates that the Shield lakes and limestone-transition lakes are described by two distinct relationships where the rate of oxygen loss per unit oxygen concentration is greater in the limestone-transition lakes.

By employing equation (2) or (3) to predict k from an early winter measurement of $[O_2]_m$, it is possible to estimate the logarithm of oxygen loss in a given stratum, $\log [O_2]_\Delta$ (log mg $O_2 \cdot L^{-1}$), over a specified time interval, t (d).

$$(4) \quad \log [O_2]_\Delta = k \cdot t$$

The oxygen remaining at the end of this time period, $[O_2]_r$ (mg $O_2 \cdot L^{-1}$), is the antilogarithm of the difference between $\log [O_2]_\Delta$ and $\log [O_2]_m$ (log mg $O_2 \cdot L^{-1}$).

$$(5) \quad [O_2]_r = 10^{(\log [O_2]_m \, - \, \log [O_2]_\Delta)}$$

Predicting Oxygen Profiles

Our procedure for predicting winter oxygen profiles is out-

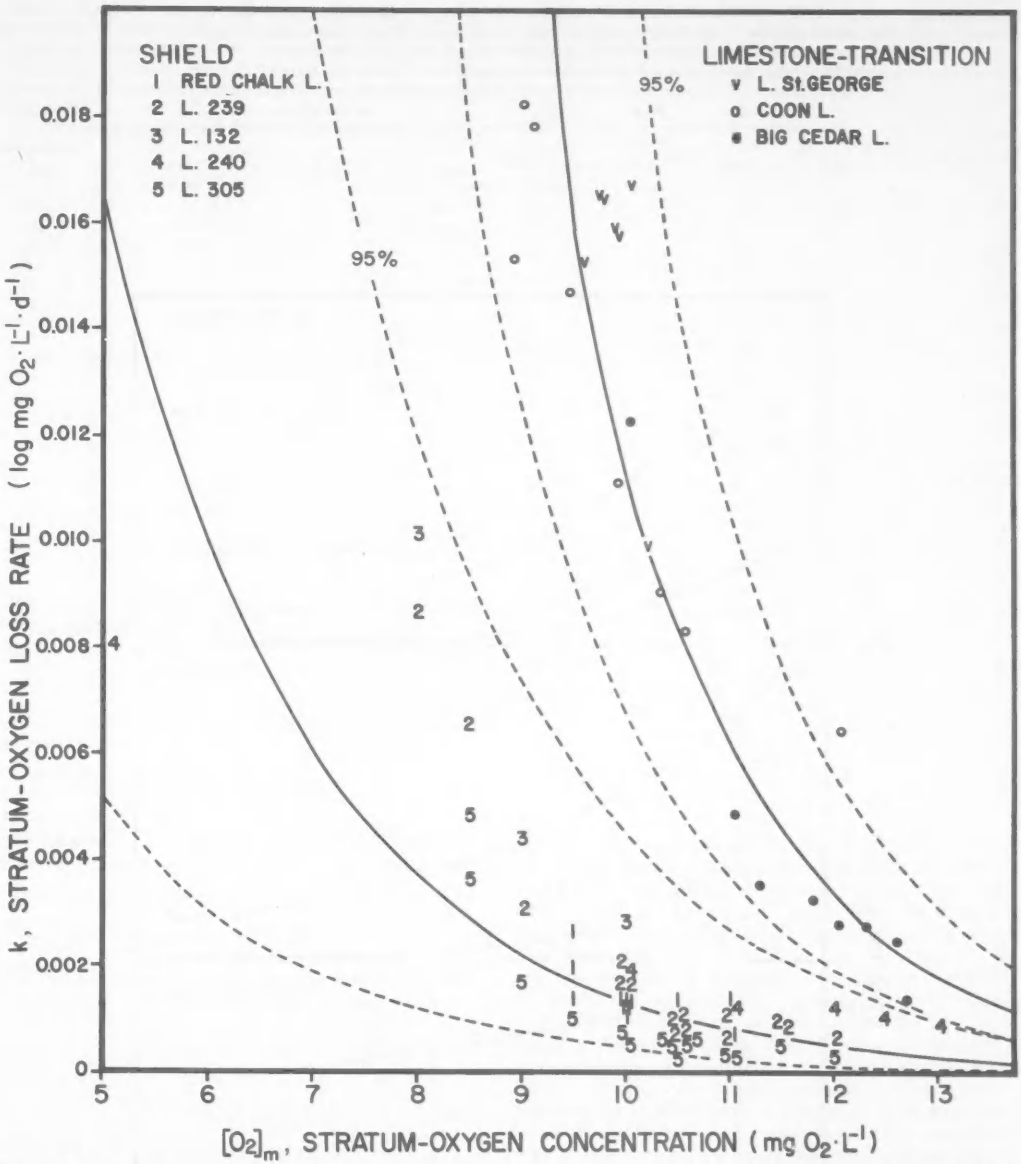

FIG. 1. Change in stratum-oxygen concentration near ice cover (1 m) and near bottom (13–15 m) in the study lakes, 1977–78. Fitted semi-log regression lines and respective slopes, k, (i.e. stratum-oxygen loss rate) have been included. The printed oxygen values represent stratum-oxygen concentration 5–15 d after freeze-up, $[O_2]_m$.

lined below using Big Cedar Lake data as an example.

1. We measured an early winter oxygen profile 5–15 d after ice formation on the approximate date of maximum volume-weighted oxygen concentration for the lake (i.e. December 12, 1977). For each stratum calculations (2) through (5) were performed, in this case, for the 15-m stratum depth.

TABLE 2. Matrix of correlation coefficients, R, incorporating stratum-oxygen loss rate, k, stratum depth, D, mean depth, MD, oxygen concentration, $[O_2]_m$, seston concentration, $[S]_m$, temperature, T_m, and conductivity, C_m, for the study lakes ($n = 23$ for all R values). $^*P < 0.05$; $^{**}P < 0.01$. Subscript m indicates data were recorded 5–15 d after freeze-up.

	D	MD	$[O_2]_m$	T_m	C_m	$[S]_m$
log k	0.39	−0.41	−0.94**	0.14	0.31	0.75**
D		−0.32	−0.52	−0.83**	−0.06	0.44*
MD			0.46	−0.21	0.31	−0.16
$[O_2]_m$				−0.27	−0.21	−0.77**
T_m					−0.29	0.32
C_m						0.33

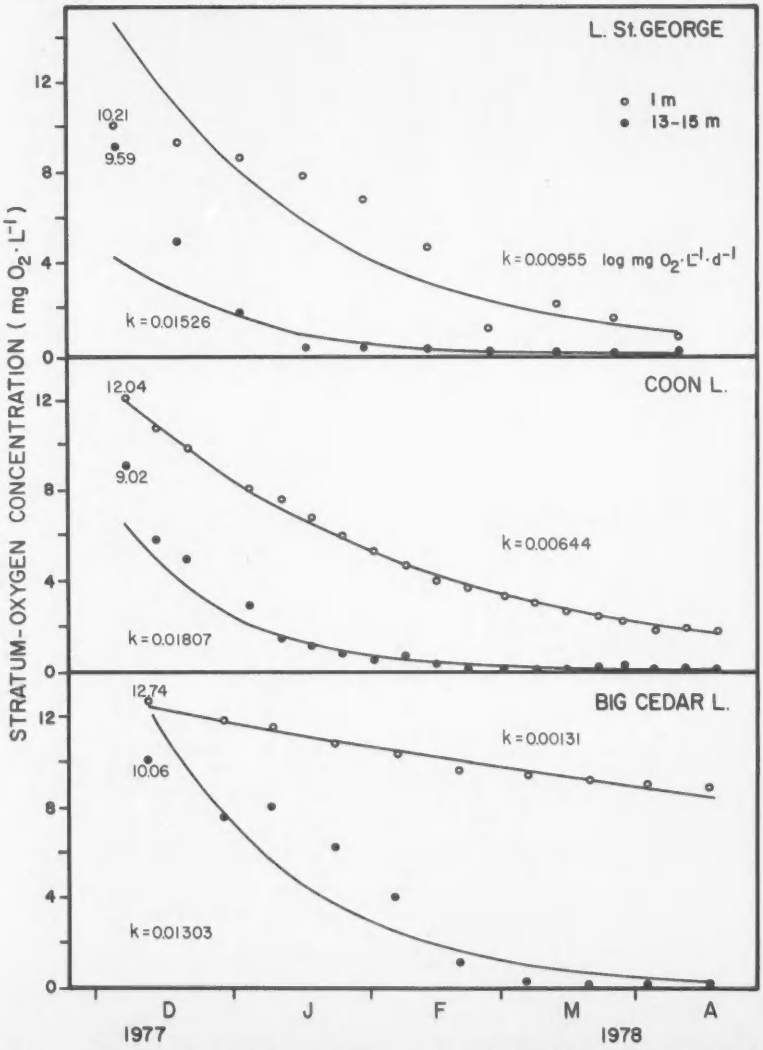

FIG. 2. Relationship between stratum-oxygen loss rate, k, and stratum-oxygen concentration 5–15 d after freeze-up, $[O_2]_m$, for the limestone-transition study lakes and five Ontario Shield lakes.

TABLE 3. Results of stepwise multiple regression analysis between the logarithm of stratum-oxygen loss rate, log k, (as the dependent variable) and stratum depth, D, mean depth, MD, oxygen concentration, $[O_2]_m$, seston concentration, $[S]_m$, temperature, T_m, and conductivity, C_m, for the study lakes ($n = 23$). $^{**}P < 0.01$. Subscript m indicates data were recorded 5–15 d after freeze-up.

Independent variable	Multiple R	F ratio
$[O]_m$	0.94	44.33**
C_m	0.95	1.82
D	0.96	0.69
MD	0.96	0.14
$[S]_m$	0.96	0.08
T_m	0.96	0.03

Stratum depth (m)	$[O_2]_m$ Dec. 12/77 (mg $O_2 \cdot L^{-1}$)
1	12.7
3	12.6
5	12.3
7	12.1
9	11.8
11	11.3
13	11.0
15	10.1

2. To calculate t between December 12, 1977, and the date for which a predicted oxygen profile is desired (i.e. April 17, 1978), we used

$$t = 126 \text{ d}$$

3. To calculate k for each stratum we substituted $[O_2]_m$ into equation (2).

$$k = 6.705 \cdot 10^{-0.2763[10.1]}$$

$$k = 0.01087 \text{ log mg } O_2 \cdot L^{-1} \cdot d^{-1}$$

4. To calculate log $[O_2]_\Delta$ between December 12 through April 17 for each stratum we substituted k and t into equation (4)

$$\log [O_2]_\Delta = 0.01087 \cdot 126$$

$$= 1.3670 \text{ log mg } O_2 \cdot L^{-1}$$

5. To calculate $[O_2]_r$ on April 17 for each stratum we substituted log $[O_2]_m$ and log $[O_2]_\Delta$ into equation (5)

$$[O_2]_r = 10^{(1.0043 - 1.3670)}$$

$$= 10^{-0.3627}$$

$$= 0.4 \text{ mg } O_2 \cdot L^{-1}$$

Therefore, the calculated oxygen concentration at 15 m in Big Cedar Lake on April 17 is 0.4 mg $O_2 \cdot L^{-1}$ (observed = 0.9 mg $O_2 \cdot L^{-1}$). The usefulness of this method is apparent by comparing observed and predicted spring oxygen profiles for three southern Ontario lakes which are not part of the original data set (Table 4). The three test lakes are all relatively small (50–70 ha) Shield lakes which, including Red Chalk Lake, have been monitored for a number of years now as part of the Ontario Government's Lakeshore Capacity Study and more recently under the auspices of the Acid Precipitation in Ontario Study. Predicted spring oxygen concentrations underestimated observed levels in Walker and Harp lakes by about 1 mg $O_2 \cdot L^{-1}$ and 2 mg $O_2 \cdot L^{-1}$, respectively. In Crosson Lake, predicted concentrations varied about ± 0.5 mg $O_2 \cdot L^{-1}$ from observed levels.

TABLE 4. Predicted, Pr, and observed, Ob, spring oxygen profiles under ice cover in three southern Ontario Shield lakes (from Ontario Ministry of the Environment, unpublished data).

Lake	Date	Depth (m)	Oxygen (mg $\cdot L^{-1}$) Pr	Ob
Walker	March 15/77	1	9.5	10.5
		3	8.8	9.0
		5	7.0	8.0
		7	7.0	7.5
		9	6.1	7.0
		11	5.2	6.0
		13	4.2	5.0
		15	2.5	4.5
Harp	March 22/77	1	8.5	10.4
		3	8.4	10.3
		5	—	9.6
		7	6.9	9.1
		9	6.5	8.9
		11	6.7	8.8
		13	6.5	8.5
		15	7.3	8.2
		17	6.2	8.5
		19	5.4	8.4
		21	5.4	7.9
		23	5.4	7.2
Crosson	March 7/77	1	9.7	9.0
		3	8.9	8.0
		5	8.1	7.5
		7	7.3	7.5
		9	7.3	7.0
		11	6.4	6.5
		13	6.4	6.0
		15	5.5	5.5
		17	5.5	5.0
		19	4.5	4.0
		21	2.8	3.5

In predicting stratum-oxygen loss rates, an oxygen profile determined less than 1 wk after ice formation would likely underestimate the observed loss rates. On the other hand, an oxygen profile measured more than 2 wk after ice formation would probably overestimate the observed loss rates. For fisheries managers, who are particularly concerned with forecasting winter-kill conditions, an oxygen profile measured at least 2 wk after ice formation should provide a safe prediction as to the date that critically low oxygen concentrations might develop.

Discussion

The oxygen concentration in a lake stratum soon after freeze-up probably represents an integration of a number of factors that ultimately limit depth-specific oxygenation/

oxidation processes under ice cover. The most important factors affecting winter oxygen loss for a given lake appear to be the effectiveness of wind-induced fall oxygenation and the oxidation/dissipation of oxidizable material prior to freeze-up and lake morphometry.

Rudd and Hamilton (1978) working on Lake 227, a small Shield lake in northwestern Ontario, showed that in years when fall oxygenation was incomplete and large quantities of methane were trapped under ice cover, whole-lake anoxia invariably developed. If we generalize from this phenomenon, it is apparent that with the onset of ice cover low oxygen concentrations and large quantities of oxidizable material favor excessive oxygen depletion. Alternatively, if oxygen concentrations are high and the supply of oxidizable material reduced, then minimal oxygen depletion is probable. For predictive purposes an oxygen profile is measured 5–15 d after freeze-up. In this way, depth-specific differences in oxygen concentration are accentuated reflecting stratum-oxygen loss rates which increase in proximity to the sediments.

Differences in stratum-oxygen loss rate per unit oxygen concentration between (and possibily within) lake types may be suggestive of dissimilarities in supplies of oxidizable material (Fig. 2). The lower rates in Shield lakes, compared with limestone-transition lakes, might indicate that the former lake type is characterized by oxidizable material that is relatively lesser in quantity and/or more retractory in quality. To improve the usefulness of the method presented here, we recommend investigation and confirmation of factors affecting winter oxygen loss in a variety of lake types.

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AMERICAN PUBLIC HEALTH ASSOCIATION. 1965. Standard methods for the examination of water and waste-water. 12th ed. American Public Health Association, New York, NY. 769 p.

BARICA, J., and J. A. MATHIAS. 1979. Oxygen depletion and winter-kill risk in small prairie lakes under extended ice cover. J. Fish. Res. Board Can. 36: 980–986.

CASSELMAN, J. M., and H. H. HARVEY. 1975. Selective fish mortality resulting from low winter oxygen. Verh. Int. Verein. Limnol. 19: 2418–2429.

GREENBANK, J. 1945. Limnological conditions in ice-covered lakes, especially as related to winter-kill of fish. Ecol. Monogr. 15: 344–392.

JACKSON, M. B. 1979. Winter oxygen loss in three southern Ontario lakes. M.Sc. thesis, Watershed Ecosystem Program, Trent University, Peterborough, Ontario.

RUDD, J. W. M., and R. D. HAMILTON. 1978. Methane cycling in a eutrophic shield lake and its effects on whole lake metabolism. Limnol. Oceanogr. 23: 337–348.

SCHINDLER, D. W. 1971. Light, temperature, and oxygen regimes of selected lakes in the experimental lakes areas, Northwestern Ontario. J. Fish. Res. Board Can. 28: 157–169.

WELCH, H. E. 1974. Metabolic rates of arctic lakes. Limnol. Oceanogr. 19: 65–73.

WELCH, H. E., P. J. DILLON, and A. SREEDHARAN. 1976. Factors affecting winter respiration in Ontario lakes. J. Fish. Res. Board Can. 33: 1809–1815.

WOODS, D. E. 1961. The effects of compressed air on winter oxygen levels in a fertile southern Minnesota lake. Minnesota Fish Game Invest. 3: 51–68.

Ability of Standard Toxicity Tests to Predict the Effects of the Insecticide Diflubenzuron on Laboratory Stream Communities

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HANSEN, S. R., AND R. R. GARTON. 1982. Ability of standard toxicity tests to predict the effects of the insecticide diflubenzuron on laboratory stream communities. Can. J. Fish. Aquat. Sci. 39: 1273–1288.

We assessed the ability of a standard set of freshwater single-species toxicity tests to predict accurately effects of the insecticide diflubenzuron (1-(4-chlorophenyl)-3-(2,6-difluorobenzoyl)urea) on complex laboratory stream communities. The single-species tests complied with requirements prescribed for establishing freshwater quality criteria and included nine freshwater animal acute tests, five freshwater animal chronic tests, and one freshwater algal test. The stream communities were stocked from a natural source, equilibrated for 3 mo and then treated with diflubenzuron for 5 mo. Effects on these stream communities were assessed at the functional group level using biomass and diversity for the analysis. The single-species tests adequately predicted the concentrations of diflubenzuron which affected these stream communities; the most-sensitive test species, insects and crustaceans, were up to an order of magnitude more sensitive than the observed community effects. The single-species tests were less successful in predicting the exact nature of the community level effects. Those effects resulting from direct lethality to component species were clearly predicted; indirect effects due to altered interspecies interactions could only be predicted with an a priori knowledge of the system's trophic dynamics.

Key words: toxicity, diflubenzuron, streams, community effects, toxicity testing

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Nous avons évalué la capacité d'une série d'essais de toxicité standard avec espèces uniques à prédire correctement les effets de l'insecticide diflubenzuron (1-(4-chlorophényl)-3-(2,6-difluorobenzoyl) urée) sur des communautés fluviatiles complexes en laboratoire. Ces essais sont conformes aux normes de définition des critères de qualité de l'eau douce et comportent neuf essais aigus, cinq essais chroniques et un essai avec algues, tous organismes dulçaquicoles. Les communautés, provenant de source naturelle, ont été équilibrées pendant 3 mois et ensuite traitées au diflubenzuron pendant 5 mois. Nous avons évalué les effets sur ces communautés au niveau de groupe fonctionnel, en fondant l'analyse sur la biomasse et la diversité. Grace à ces essais, on peut prédire convenablement les concentrations de diflubenzuron qui influencent ces communautés; les effets sont plus prononcés sur les espèces les plus sensibles, insectes et crustacés, que sur la communauté, et ce d'un facteur allant jusqu'à un. Par ailleurs, les essais avec espèces uniques ne permettent pas de prédire avec autant de succès la nature exacte des effets au niveau de la communauté. Les effets résultant d'une létalité directe à l'endroit des espèces constituantes sont clairement prédits; les effets indirects découlant de modifications des interactions entre espèces ne peuvent être prédits qu'avec une connaissance a priori de la dynamique trophique du système.

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THE normal functioning of a freshwater aquatic biological community is in part a result of its species composition and the state of the interactions between these component species. These two factors are coupled in a complex manner, not easily modeled or quantified. When toxic substances enter natural aquatic systems, both underlying factors can be affected, resulting in altered community structure and function.

Currently, in the development of freshwater quality criteria, the potential of a substance to harm natural aquatic communities is assessed primarily by examining direct toxic effects on a prescribed set of single-species populations, using

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methods published in the United States Federal Register on March 15, 1979 (44FR15926), July 25, 1979 (44FR43660), and October 1, 1979 (44FR56628). In these tests, organisms are exposed to the suspected toxicant and alterations in population level parameters (i.e. mortality, fecundity, and growth rate) are used as the effect criteria. Indirect toxic effects due to altered interspecies or intraspecies interactions are not considered.

Because of the urgency of water pollution problems, the use of these single-species tests has gained wide acceptance. They are simple, provide rapid generation of data, and ecological significance of the results is apparent. However, considerable uncertainty has been expressed concerning the ability of these single-species tests to predict accurately actual effects which would be experienced in natural complex biological communities (Mount 1979, 1981; Cairns 1980; Gibson 1981; Reisa 1981). This uncertainty arises because of a number of basic assumptions which are inherent in the sole use of these tests in setting water quality standards. First, it is assumed that the standard test species exhibit a range of sensitivities sufficient to protect most, if not all, species in natural assemblages. Second, it is assumed that interactions between species need not be considered separately. Either these interspecies interactions are adequately protected by single-species test results (i.e. the sensitivity of the interactions is equal to, or less than, the sensitivity of the single-species population parameters) or, if the interactions are more sensitive, the alterations in these interactions have little impact on the funtion and structure of the community. It has been suggested that the use of more complex test systems may reduce these deficiencies associated with single-species tests, and therefore, produce more predictive results (Heath 1979; U.S.E.P.A. 1981; N.R.C. 1981). These proposed complex systems offer the advantages of simultaneously testing large numbers of species and including interactions between species in their assessment of toxicity. However, because of high cost, slow generation of data, and ambiguous ecological significance of results, their use in criteria development has been retarded and reliance on single-species tests continues.

The ability of these standard single-species toxicity tests to predict aquatic community level effects has received only limited direct experimental confirmation. In a few studies, for a limited number of toxic substances, comparisons have been made between the results generated in standard single-species tests and in laboratory or field community level systems (Eisele and Hartung 1976; Hitchock 1965; Geckler 1976; Weiss 1976). In each case, the results generally support the adequacy of single-species tests. Concentrations of toxicants that cause community level effects are within an order of magnitude of those concentrations predicted as harmful by the standard bioassays. However, the nature of the community level effects was often not well predicted. None of these studies are critical tests of the predictive ability of the single-species tests. The studies either do not include the complete prescribed set of test species, and/or they fail to monitor sufficiently the structure and function of the entire biological community.

The objective of this study was to examine more critically the predictive ability of the single-species tests and, therefore, to test the validity of their underlying assumptions. The strategy was to determine effect levels of the insecticide diflubenzuron (1-(4-chlorophenyl)-3-(2,6 difluorobenzoyl)urea), a chitin synthesis inhibitor, on a standard set of freshwater test organisms and to compare the results with effects observed in complex laboratory stream communities. Comparisons of effect concentrations and the nature of such effects were then used to assess predictive ability.

Materials and Methods

These studies were conducted at the U.S. Environmental Protection Agency's Corvallis Environmental Research Laboratory in Corvallis, OR. The duration of the stream study was ~9 mo, August 1979–May 1980. The single-species toxicity tests were performed June–September 1980.

Standard Single-Species Tests

In this study, the set of single-species toxicity tests was chosen according to the guidelines established for deriving freshwater quality criteria, as published in the U.S. Federal Register on March 15, 1979 (44FR15970). These guidelines require the use of at least eight animal acute tests, three animal chronic tests, and one freshwater algal test. The acute toxicity tests must incorporate freshwater animal species representing eight different families, including at least one salmonid fish, one non-salmonid fish, one planktonic crustacean, one benthic crustacean, one benthic insect, and one benthic insect detritivore. The chronic tests must incoroporate three aquatic animal species, including at least one fish, one invertebrate, and at least one of the three must be a freshwater species.

The actual set of single-species toxicity tests used in this study met these guideline requirements and included nine animal acute tests (Table 1), five animal chronic tests, and one freshwater algal test (Table 2). These tests employed standard exposure and analysis methods (ASTM 1980; U.S.E.P.A. 1975; Nebeker 1973; Garton 1980; Andros and Garton 1980); more detailed descriptions of the methods and results are not yet published (A. Nebeker and G. Chapman, U.S. Environmental Protection Agency, Environmental Research Laboratory, Corvallis, OR). Where applicable, life stages were chosen so that a molt would occur during the test period, thus ensuring the inclusion of effects on chitin synthesis in the toxicity assessment.

The determinations of effects in these single-species tests were made at the population level. The parameters of analysis are survival in the acute tests and survival, fecundity, and growth in the chronic tests. Reductions in these parameters are assumed to indicate direct toxic effects.

The maximum concentration of diflubenzuron used in these tests varied between 50 and 90 μg/L, resulting from changes in experimental conditions (e.g. water temperature) during the course of the study. Analysis of the concentration of diflubenzuron in the water of each test system was performed throughout the test period by high-pressure liquid chromatography, using a single-band 254-nm UV detector, a micro-Bondapak C-18 column, and a 60:40 acetonitrile–water mobile phase. Because of the sensitivity limit of the analysis procedure, reported concentrations ≥1.0 μg/L are measured

TABLE 1. Acute toxicity tests using insecticide diflubenzuron.

Factors	Steelhead trout (*Salmo gairdneri*)	Fathead minnow (*Pimephales promelas*)	Guppy (*Lebistes reticulatus*)	Midge (*Cricotopus* sp.)	Midge (*Tanytarsus dissimilis*)	Gammarid (*Hyallela azteca*)	Daphnia (*Daphnia magna*)	Snail (*Juga plicifera*)	Snail (*Physa* sp.)
Class of test species	Salmonid fish	Non-salmonid fish	Non-salmonid fish	Benthic insect	Benthic detritivore insect	Benthic crustacea	Planktonic crustacea	Freshwater mollusk	Freshwater mollusk
Initial age of organisms	5 mo	2 mo	30 d	—	—	—	24 h	—	1.5 mo
Initial size or developmental stage	58 mm	35 mm	—	4th instar	2nd instar	2–4 mm	—	3–6 mm	12–20 mm
Test duration	96 h	96 h	96 h	7 d	5 d	5 d	48 h	96 h	7 d
Flow type	Flow through	Flow through	Flow through	Flow through	Flow through	Flow through	Static	Flow through	Flow through
Criteria for effect determination	Survival LC50	Survival LC50	Survival LC50	Molting success	Molting success	Survival LC50	Survival LC50	Survival LC50	Survival LC50
Water temp. (°C)	11	20	20	20	20	20	20	20	20
Water hardness (mg/L as $CaCO_3$ equiv.)	24	25	25	25	25	25	50 100 100	25	25

TABLE 2. Chronic toxicity tests using insecticide diflubenzuron.

Factors	Steelhead trout (*Salmo gairdneri*)	Fathead minnow (*Pimephales promelas*)	Daphnia (*Daphnia magna*)	Algae (*Selenastrum capricornutum*)	Snail (*Juga plicifera*)	Snail (*Physa* sp.)
Class of test species	Salmonid fish	Non-salmonid fish	Planktonic crustacea	Freshwater algae	Freshwater mollusk	Freshwater mollusk
Initial age of organisms	5 h postegg fertilization	Egg	24 h	Exponential growth	—	1.5 m
Initial size or developmental stage	—	—	—	—	3–6 mm	12–20 mm
Test duration	9 wk (including 6 wk posthatch exposure with 4 wk of feeding	30 d	21 d	120 d	2 wk	2 wk
Flow type	Flow through	Flow through	Static	Static	Flow through	Flow through
Criteria for effect determination	Survival, growth	Survival, growth	Survival, reproduction	Population, growth (dry weight)	Survival, growth	Survival, growth, reproduction
Water temp. (°C)	11	20	20	24	20	20
Water hardness (mg/L as $CaCO_3$ equiv.)	25	25	50	—	25	25

values, whereas those concentrations <1.0 μg/L are nominal values (Corley et al. 1974; Oehler and Holman 1975).

Complex Laboratory Stream Community Tests

Community level studies were carried out in 10 indoor continuous-flow laboratory stream channels (Fig. 1). Rocks, 7.5–13.0 cm in diameter, were added to the riffle portions of each channel to a depth of ~15 cm; no rocks were placed in the pool areas. Well water (see Samuelson 1976 for a detailed history of water quality) was added continually at a rate of 5 L/min and maintained at a depth of 10 cm above the rocks by means of standpipes, establishing a 95% replacement rate of 4.5 h. A midstream surface current of 30 cm/s was maintained by using stainless steel, motordriven paddle wheels. A uniform light intensity of 2.2×10^3 lx (200 ft. candles) was maintained over each channel, using suspended metal halide lamps (Maxi-Gro, 1000 W, Sylvania GTE Agronomics, Waltham, MA.[2]) A natural diurnal light cycle was set with 30-min dawn-and-dusk low light periods.

The fauna were introduced into the stream channels through the replacement water supply and via field collections. Introductions via the water inflow were continuous, but limited to microorganisms (i.e. primarily algae and bacteria). Periodic field collections supplied more diverse fauna. During August–October 1979, biological collections were made twice weekly from Rock Creek, a second-order forest stream in the Mary's River watershed, 16 km west of Corvallis, OR. A combination of kicking and rock-brushing techniques dislodged organisms and facilitated net collections. After removing fish and crayfish, the field samples were randomly distributed among the 10 stream channels. Fish and crayfish were eliminated to maintain the viability of the insect fauna of these stream communities. The large energy demands of even a few of these predators coupled with the lack of insect immigration into these laboratory systems would quickly devastate the insect populations and prevent longterm assessments of diflubenzuron impact on this group.

Detrital material, essential as a food source for the stream decomposers, was manually introduced into the channels. In the field collections, varying amounts of leafy and woody material were also trapped. This detritus was distributed among the channels, adding an estimated 50–100 g of allochthonous material per stream per sampling event. After this initial stocking, monthly supplements of 50 g of freezer-preserved dead alder (*Alnus* sp.) leaves were added to each channel.

In all 10 laboratory channels, the biota were allowed to develop and equilibrate for 3 mo (September–November

[2]Mention of product does not constitute endorsement by the U.S. Environmental Protection Agency.

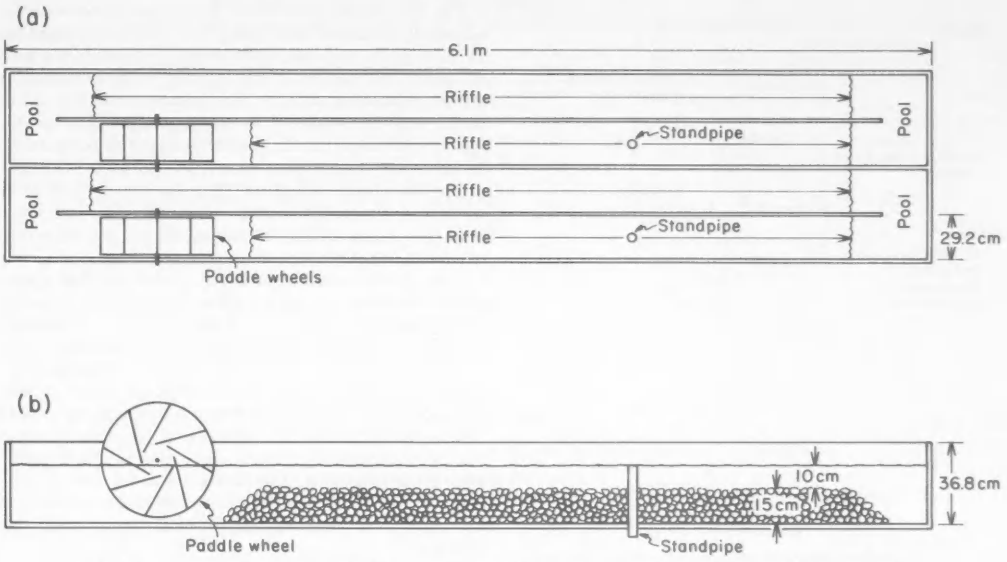

FIG. 1. Laboratory stream channels: (a) an overview of a pair of channels; (b) a side view of a single channel.

1979). Equilibration involved the establishment, in all streams, of similar diversity and biomass for each of the component functional groups (Fig. 3–9). The channels were then separated into five pairs, and diflubenzuron treatments were carried out for the following 5 mo (December 1979–May 1980). Four stream pairs received continuous addition of diflubenzuron; each pair received one concentration of either 0.1, 1.0, 10, or 50 μg/L. Dimethylformamide (DMF) served as the carrier solvent and was maintained at 1 mg/L in all treatment streams. The fifth stream pair served as carrier controls, with continuous addition of 1 mg/L of DMF. The chemical characteristics of the water in the 10 stream channels were monitored throughout the study. Water temperature was measured continuously; diflubenzuron concentration, pH, D.O., hardness, and alkalinity weekly; and monthly measurements were taken of nitrate, nitrite, ammonia, organic nitrogen, and orthophosphate.

The biota in each stream were estimated monthly throughout the October 1979–May 1980 study period. Three samples were taken from each channel; each sample was collected by sealing off a 0.052-m^2 area, dislodging attached organisms, and siphoning out the enclosed water and suspended organisms. Samples were divided for analyses of the composition and biomass of the invertebrate, algal, fungal, and bacterial components.

The composition of the invertebrate fauna was estimated by filtering the stream samples through a Tyler 115-mesh metal screen and identifying the collected organisms. Insects other than the dipteran family Chironomidae were identified to at least the genus level. The Chironomidae were identified to family, subfamily, or tribe.

The biomass of each invertebrate functional group was estimated by the total cumulative length of all sampled organisms taxonomically assigned to that group. The use of these cumulative lengths as biomass estimates are, undoubtedly, approximations; however, we feel they are adequate for these between-stream comparisons. Because of differences in geometry between the genera comprising each functional group, the use of genus-specific weight/length regressions would have been preferable in producing the most accurate estimates. Unfortunately, such regressions do not exist for a large number of the genera in question. However, preliminary data generated from other very similar stream communities (C. Callahan, U.S. Environmental Protection Agency, Environmental Research Laboratory, Corvallis, OR., personal communication) support the validity of our approximation. Regressions of the total cumulative weight of mixed genus invertebrate samples against the cumulative length of such samples produced results for invertebrates that were statistically significant at the 95% level of confidence.

The composition of the diatom flora, which represented ~80% of all algae in the streams, was estimated from slide preparations. Each sample was blended and an aliquot evaporated onto a glass slide. The organic matter was burned off, and the remaining silica valves were mounted in Hyrax. Microscopic identifications (1000×, oil immersion) to at least the genus level of the first 100 randomly encountered cells were used to estimate relative abundances in each channel and to calculate diversity.

An estimate of algal biomass was made from the determination of the chlorophyll *a*, *b*, *c*, and pheophytin concentrations in each stream channel. Each sample was blended, treated with $MgCO_3$, and centrifuged. The precipitate was dissolved in 90% acetone, sonicated, and centrifuged. The resulting supernatant was analyzed spectrometrically at 750, 663, 645, and 630 nm. A trichromatic procedure was used to dif-

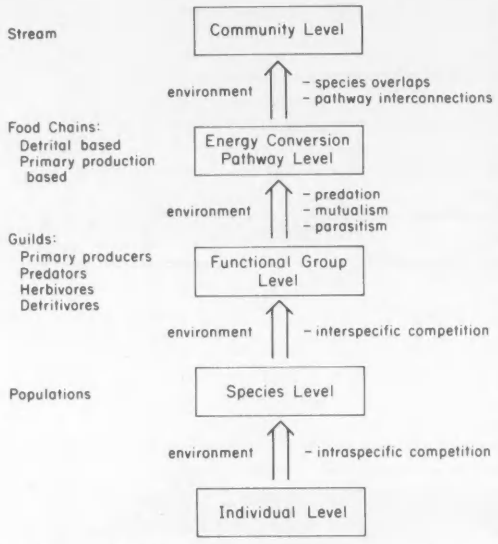

FIG. 2. Hierarchical levels of investigation of a stream community.

ferentiate between chlorophyll *a*, *b*, and *c* (Weber 1973). A monochromatic procedure was used for pheophytin determination (Weber 1973).

The biomass of the fungal flora in each stream channel was estimated on a relative basis from measurements of hyphal abundance on leaf material. A 5.0-g pack of dead alder leaves was prepared, incubated for 6 wk in the channel, removed, and cut into 0.5-cm discs. Ten of these discs were randomly selected, clarified with 5% KOH, hardened with 50% ethanol, and stained with lactophenol-trypan blue (Commonwealth Mycological Institute 1968). Using an ocular micrometer, we estimated the percent cover of hyphae on the leaf surface.

The composition of the fungal flora in each stream channel was estimated from an analysis of spores on the leaf packs. Twenty leaf discs were incubated overnight in filter-sterilized water to stimulate spore formation. These discs were then fixed in lactophenol. Microscopic identification (250×, phase contrast) of spores on the periphery of each disc was used to estimate species abundances and calculate diversity (Peterson 1962, 1963a, b; Ingold 1942; Ingold and Cox 1957; Ranzoni 1953). This procedure is qualitative at best because of the uncertain relationships between hyphal abundance and spore formation.

The composition and biomass of the bacterial flora in each stream channel were estimated from a sequence of dilution plating, morphological sorting, and classification testing. A 1.0-mL blended aliquot from each stream sample was serially diluted, plated on PYG media, and incubated for 48 h at 20°C. Colonies were counted and typed according to morphological characteristics. When possible, each type was identified to genus by use of dichotomous testing procedures (Buchanan and Gibbons 1974; Shayegani et al. 1976; Steele 1979). Bacterial biomass was assumed directly proportional to cell density and expressed as cells/mL.

The determination of effects in the stream communities was made at the functional group level (Merritt an Cummins 1978) (Fig. 2). Each functional group is composed of a guild of species that perform a specific step in the community's energy processing pathway. The structure and function of each group is a result of its species composition and the interactions among its component species (e.g. competition) as well as the interactions among functional groups (i.e. predation, mutualism, parasitism, etc.). Analysis at this level of complexity is appropriate because it incorporates both direct toxic effects and indirect interaction effects, and the results are clearly transferable to the community level.

Each month, identified taxa were placed into their appropriate functional group(s): either invertebrate scrapers, invertebrate shredders, invertebrate predators, invertebrate collectors–gatherers–filterers, algal primary producers, bacterial decomposers, or fungal decomposers. Using diversity (Shannon's index, H') and biomass as the parameters of analysis, comparisons were made between treatment and control streams. Reduction in the biomass of a functional group is assumed indicative of a lowered processing rate for its particular energy processing step. Reduction in the diversity of a functional group is assumed indicative of reduced stability of the guild as a result of simplification of its underlying structure.

Throughout the study period, between-stream comparisons were made. The parameters of analysis were biomass and diversity of each of the functional groups. During the equilibration period, the equivalence of the 10 stream channels was assessed. For each test parameter, an analysis of variance and, subsequent, pairwise Student–Neuman–Keuls multiple-range tests were performed. During the treatment period, the existence of differences between the four treatment levels and the controls were assessed. For each test parameter, a Williams' test (Williams 1972) was performed, using average stream values for each of the two replicates per treatment level.

The experimental design used for the analysis of the data was a completely randomized design with subsampling (Steel and Torrie 1960). Sampling error determined from the within-stream samples was small compared to experimental error determined from variation between streams treated alike. This latter experimental error was the variance that was used to estimate the standard error of a treatment effect and was used in further analysis of the data using Student–Neuman–Keul's test and Williams' test (Williams 1972).

Results

SINGLE-SPECIES TOXICITY TESTS

The results from the acute (Table 3) and chronic (Table 4) toxicity tests reveal that insect and crustacean species were affected by diflubenzuron. Values for the LC50 ranging from 1.0 to 1.8 μg/L were determined for four insect and crustacean species. No acute response resulted for fish or molluskan species from exposure to the highest concentration tested (45 μg/L). A chronic effect level was obtained for only *Daphnia magna* (0.06 μg/L). No chronic effects were observed for fish, an alga, and the two mollusks tested at

TABLE 3. Acute toxicity test results with insecticide diflubenzuron.

Test species	Test description	LC50 (μg/L)	95% confidence level
Salmo gairdneri	Salmonid fish species — 96 h LC50	No effect ≤45	
Pimephales promelas	Non-salmonid fish species — 96 h LC50	No effect ≤45	
Lebistes reticulatus	Non-salmonid fish species — 96 h LC50	No effect ≤45	
Cricotopus sp.	Benthic insect species — 4th larval instar to pupae LC50	1.79	(1.48, 2.13)
Tanytarsus dissimilis	Benthic detritivore insect species — 2nd to 3rd larval instar LC50	1.02	(0.56, 1.47)
Hyallela azteca	Benthic crustacean species — 96 h LC50	1.84	(0.05, 3.71)
Daphnia magna	Planktonic crustacean species — 48 h LC50		
	Total hardness (mg/L)		
	200	4.42	(2.79, 8.63)
	100	6.89	(3.98, 18.50)
	50	4.55	(2.58, 12.71)
Juga plicifera	Freshwater molluskan species — 96 h LC50	No effect ≤45	
Physa sp.	Freshwater molluskan species — 96 h LC50	No effect ≤45	

TABLE 4. Chronic toxicity test results with insecticide diflubenzuron.

Test species	Test description	LC50 (μg/L)	95% confidence level
Salmo gairdneri	Salmonid fish species — survival and growth in early life stages (30 d)	No effect ≤45	
Pimephales promelas	Non-salmonid fish species — survival and growth in early life stages (30 d)	No effect ≤45	
Daphnia magna	Planktonic crustacean species — survival and reproduction in a full life cycle	0.062	(0.051, 0.071)
Selenastrum capricornutum	Freshwater algal species — growth after a 120-h exposure	No effect ≤45	
Juga plicifera	Freshwater molluskan species — survival, growth, and reproduction after a 3-wk exposure	No effect ≤45	
Physa sp.	Freshwater molluskan species — survival, growth, and reproduction after a 3-wk exposure	No effect ≤45	

concentrations as high as 45 μg/L. Using the "Guidelines for Deriving Water Quality Criteria for the Protection of Aquatic Life and its Uses," Federal Register 44FT15970 (March 15, 1979), a final acute toxicity value of 1.1 μg/L and a final chronic toxicity value of 0.06 μg/L were established.

LABORATORY STREAM COMMUNITIES

The taxa found in these laboratory stream systems and their functional group assignments are presented in Appendix 1. Organisms found in the stream samples were sorted using these lists of taxa and, subsequently, calculations of diversity and biomass for each functional group were made. Many genera were placed into more than one functional group because of the diversity of trophic function exhibited by different species within a single genus, as well as the variety of trophic functions exhibited by individual species. Table 5 shows the in-stream responses of the most common of these taxa to diflubenzuron exposure. These sensitivities coupled with the above functional assignments were used to elucidate the mechanisms underlying alterations in each functional group.

In general, the invertebrate functional groups were the most severely impacted, experiencing rapid and permanent reductions in their biomass and diversity when exposed to ≥1.0 μg/L of diflubenzuron (Fig. 3–6). These effects were the result of major reductions in many of their component aquatic insect populations, primarily among the mayflies, stone flies, and dipterans. Effects on the important caddis fly populations could not be determined as a result of their precipitous decline during the early stages of the experiment in both control and treatment streams. This situation was apparently due to a combination of adult emergence of some species and the failure of others to become established in these laboratory systems. In all groups, diversity showed an apparent graded dose–response relationship, with little or no reductions occurring at 0.1 μg/L, intermediate reductions at 1.0 μg/L, and maximal reductions at ≥10.0 μg/L. The intermediate effects at 1.0 μg/L were apparently due to the relative insensitivity of some dipteran taxa to 1.0 μg/L, but their

TABLE 5. Effect of diflubenzuron on the most abundant stream invertebrates

	Pretreatment density (No./m²)	Pretreatment biomass (total mm/m³)	Fate in control stream	Fate in treatment streams: Concn. of diflubenzuron (μg/L)	Fate in treatment streams: Effect
Ephemeroptera					
Baetis spp.	36.0	57.2	No change in 5 mo	≥1.0	Eliminated in 1 mo
				0.1	Same as control
Epeoris spp.	26.7	44.8	Reduced ~50% in 5th mo	≥10.0	Eliminated in 1 mo
				≤1.0	Same as control
Rithogena spp.	16.4	90.6	Reduced ~50% in 2nd mo	≥1.0	Eliminated in 1 mo
			Eliminated in 4 mo	0.1	Same as control
Paraleptophlebia spp.	30.2	91.2	Reduced ~75% in 5th mo	≥1.0	Eliminated in 1 mo
				0.1	Same as control
Ephemerella spp.	46.4	94.6	Reduced ~60% in 2nd mo	≥1.0	Eliminated in 1 mo
			Reduced ~90% in 5th mo	0.1	Same as control
Plecoptera					
Peltoperla spp.	1.8	3.0	Eliminated in 4 mo	≥1.0	Eliminated in 1 mo
				0.1	Same as control
Pteronarcys spp.	0.9	3.3	Eliminated in 4 mo	≥1.0	Eliminated in 1 mo
				0.1	Same as control
Nemoura spp.	16.4	53.6	Reduced ~50% in 2nd mo	≥1.0	Eliminated in 1 mo
			Eliminated in 5 mo	0.1	Same as control
Acroneuria spp.	5.0	33.4	No change in 5 mo	≥1.0	Reduced ~90% in 3rd mo
					Eliminated in 4 mo
				0.1	Same as control
Hesperoperla spp.	3.4	26.5	No change in 5 mo	≥1.0	Reduced ~50% in 3rd mo
					Eliminated in 5 mo
				0.1	Same as control
Isoperla spp.	0.6	1.7	No change in 5 mo	≥1.0	Eliminated in 1 mo
				0.1	Same as control
Alloperla spp.	13.0	48.6	Reduced ~70% in 3rd mo	≥1.0	Reduced ~60% in 1st mo
					Eliminated in 3 mo
				0.1	Same as control
Diptera					
Chironomini	27.6	163.6	No change in 5 mo	≥10.0	Reduced ~10–75% in 1st–4th mo
					Eliminated in 5 mo
				≤1.0	Same as control
Tanytarsini	18.4	42.4	No change in 5 mo	≥10.0	Reduced ~50–95% in 1st–4th mo
					Eliminated in 5 mo
				≤1.0	Same as control
Tanypodinae	17.0	54.4	No change in 5 mo	≥10.0	Reduced ~60–95% in 2nd–4th mo
					Eliminated in 5 mo
				≤1.0	Same as control
Orthocladiinae	37.4	87.8	Reduced ~90% in 5th mo	≥10.0	Reduced ~30–75% in 1st–4th mo
					Eliminated in 5 mo
				1.0	Reduced ~50–90% in 2nd –5th mo
				0.1	Same as control
Tricoptera					
Rhydcophila spp.	5.6	32.8	Reduced ~50% in 3rd mo	≤50.0	Not significantly different from control
			Eliminated in 4 mo		
Hydropsyche spp.	2.5	15.6	Eliminated in 3 mo	≤50.0	Not significantly different from control
Micrasema spp.	1.0	2.3	Eliminated in 5 mo	≤50.0	Not significantly different from control
Coleoptera–Elmidae					
Heterlimnius spp.	5.2	15.7	No change in 5 mo	≤50.0	Same as control
Optioservus spp.	20.7	61.8	No change in 5 mo	≤50.0	Same as control
Zaitzevia spp.	1.7	5.0	No change in 5 mo	≤50.0	Same as control
Narpus spp.	1.5	4.9	No change in 5 mo	≤50.0	Same as control

TABLE 5 (*Concluded*)

	Pretreatment density (No./m²)	Pretreatment biomass (total mm/m³)	Fate in control stream	Fate in treatment streams: Concn. of diflubenzuron (μg/L)	Fate in treatment streams: Effect
Oligochaeta	52.2	92.3	Increased ~200% in 2nd–5th mo	≥10.0	Increased ~2000% in 2nd and 3rd mo Reduced ~95% in 4th mo
Gastropoda *Juga* spp.	20.9	134.9	No change in 5 mo	≤50.0	Same as control

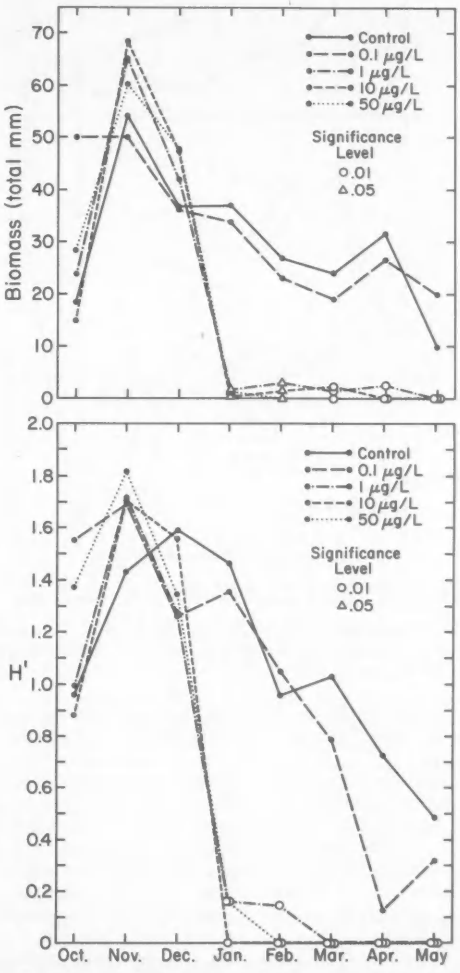

FIG. 3. Effects of diflubenzuron on the biomass (total cumulative length of organisms/m²) and the diversity (H') of the invertebrate shredder functional group.

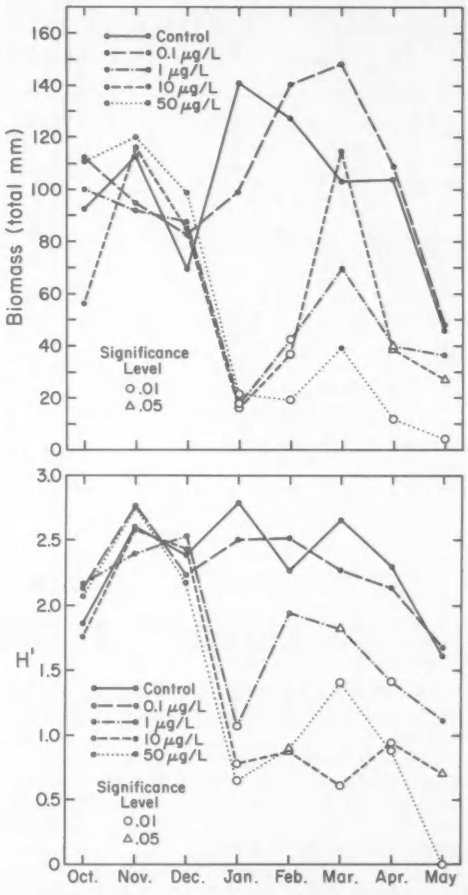

FIG. 4. Effects of diflubenzuron on the biomass (total cumulative length of organisms/m²) and the diversity (H') of the invertebrate scraper functional group.

elimination at the higher concentrations (Table 5).

This general scenario held for all of the invertebrate functional groups. However, because of differences in their

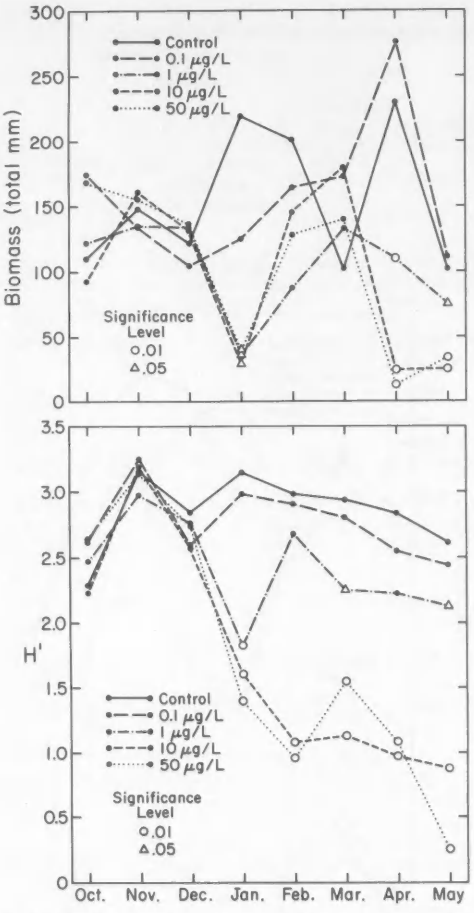

FIG. 5. Effects of diflubenzuron on the biomass (total cumulative length of organisms/m^2) and the diversity (H') of the invertebrate collector–gatherer–filterer functional group.

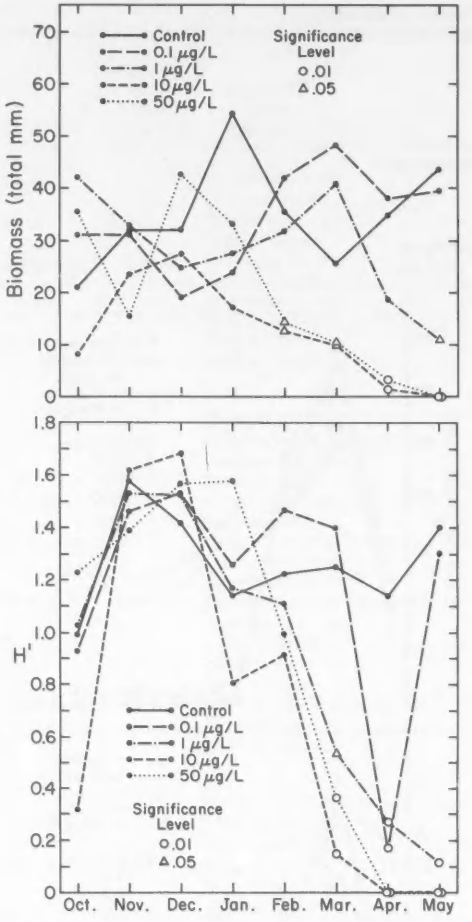

FIG. 6. Effects of diflubenzuron on the biomass (total cumulative length of organisms/m^2) and the diversity (H') of the invertebrate functional group.

species compositions (i.e. the relative abundance of dipterans in the functional group), variations between groups were apparent.

The shredder functional group (Fig. 3) was taxonomically simple, being composed mainly of mayflies and stone flies, and showed rapid and persistent effects. The graded diversity effect was not very distinct perhaps, as a result of the small dipteran component of this group.

The scraper functional group (Fig. 4) was more diverse, being composed of mayflies, stone flies, dipterans, beetles, and snails, and showed rapid, but less-persistent effects. The losses among the insect taxa were partially offset during January and February by temporary increases in the apparently insensitive snail, *Juga plicifera*, population. The riffle beetles were also insensitive and maintained their densities throughout the treatment period. The striking decline in diversity was a graded response with increasing concentration levels, primarily the result of reductions among the dipteran species.

The collector–gatherer–filterer functional group (Fig. 5), composed primarily of mayflies, stone flies, dipterans, beetles, and oligochaetes, showed rapid but discontinuous effects. In this case, the losses among the insect taxa were temporarily offset during January and February by increases in the insensitive oligochaete population. Again, because of the large dipteran component, the graded diversity response was clear.

The predator functional group (Fig. 6), being composed mainly of stone flies, dipterans, and beetles, showed slow but continuous effects. The gradual nature of these effects was the result of differences in sensitivity within the predominant

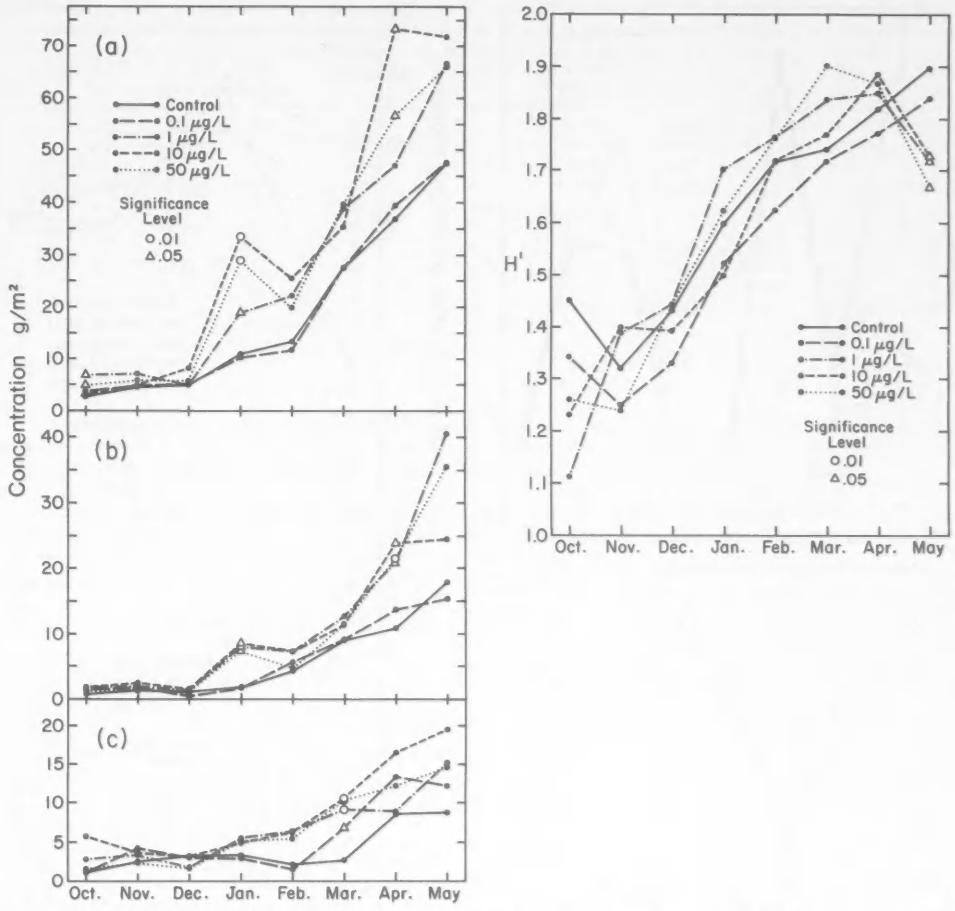

FIG. 7. Effects of diflubenzuron on the biomass (total cumulative length of organisms/m^2) and diversity of the algal primary producer functional group. Biomass is expressed as concentrations of (a) chlorophyll *a*, (b) chlorophyll *c*, and (c) pheophytin. Diversity (H') was calculated using abundances of diatom species only.

stone fly component. Some stone flies (i.e. *Pteronarcys*, *Peltoperla*, *Nemoura*, and *Isoperla*) were rapidly eliminated, whereas others (i.e. *Acroneura*, *Hesperoperla*, and *Alloperla*) required several months of treatment before elimination occurred. The genera which survived the longest also had the longest instar periods. This is not surprising, because diflubenzuron has its major effect on chitin synthesis which occurs during molts between larval instars. This functional group also shows the graded diversity response, as a result of its large dipteran component.

The algal, fungal, and bacterial functional groups (Fig. 7–9) were also impacted by the addition of diflubenzuron. In general, these groups exhibited variable and transient alterations in biomass and diversity; algae and bacteria were affected at 1.0 µg/L, and the fungi were apparently affected by as little as 0.1 µg/L.

The algal primary producer functional group (Fig. 7) experienced rapid and persisent increases in biomass and delayed reductions in diversity associated with ≥1.0 µg/L of diflubenzuron. Immediately following equilibration, all streams contained (in order of relative abundance as indicated in parentheses): *Achnanthes lanceolata* (0.38), *Navicula* sp. (0.30), *Cocconeis placentula* (0.22), *Nitzschia* sp. (0.02), *Gomphonema accuminatum* var. *coronata* (0.02), and *Rhoicosphenia curvata* (0.02). Following the start of treatment, the streams receiving ≥1.0 µg/L of diflubenzuron experienced increased densities of all taxa, plus the early appearance of *Melosira varians* and *Synedra* sp. (appearing after 2 mo of treatment, compared to 4 mo in the control); effectively raising the biomass and diversity of these streams. Toward the end of the treatment period, algal density remained high in the streams containing ≥1.0 µg/L; however,

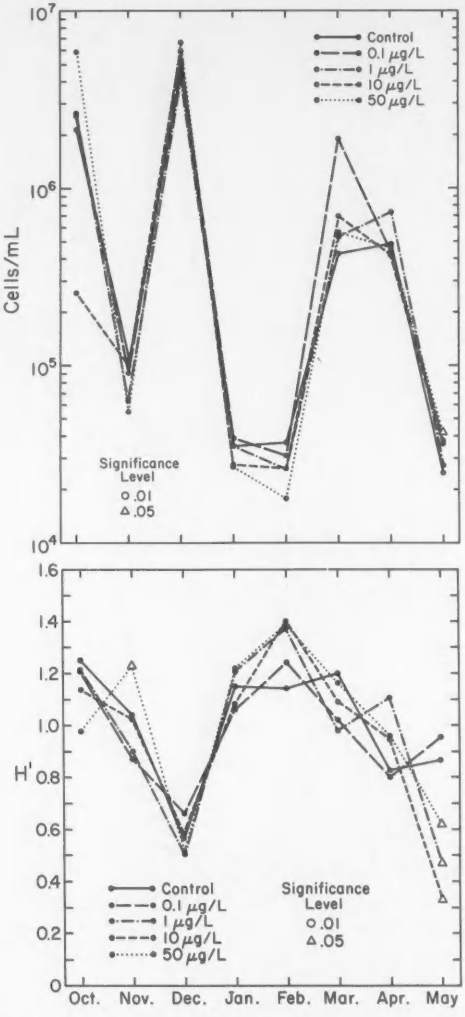

FIG. 8. Effects of diflubenzuron on the biomass (total cumulative length of organisms/m^2) and the diversity (H') of the bacterial decomposer functional group.

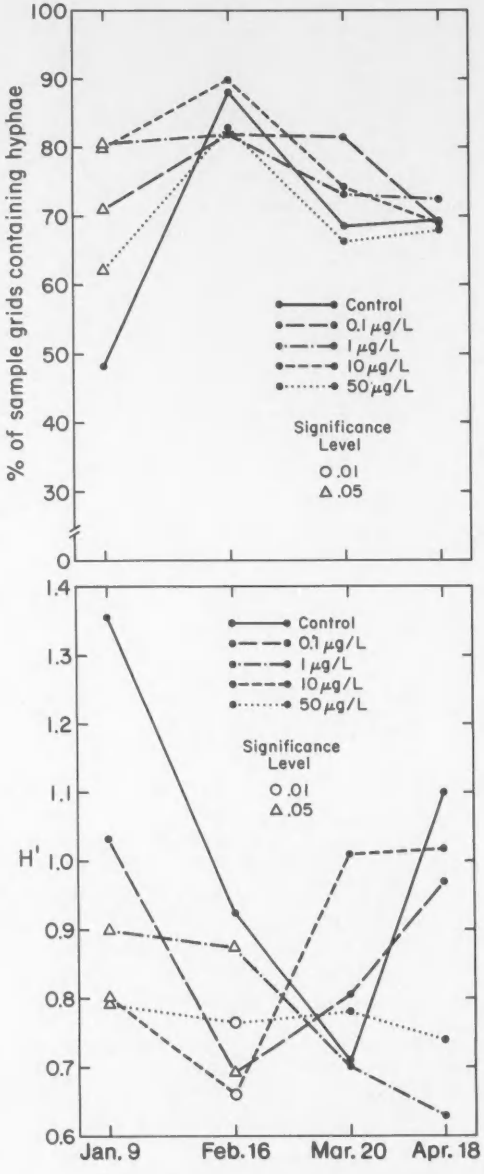

FIG. 9. Effects of diflubenzuron on the biomass (relative abundance of hyphae) and the diversity (H', using spore abundances) of the fungal decomposer functional group at four sampling periods in 1980.

M. varians and *Synedra* sp. became dominant, comprising 27% and 10%, respectively, of the overall algal abundance. Therefore, biomass remained elevated, but diversity declined.

The bacterial decomposer functional group (Fig. 8) experienced delayed reductions in diversity associated with exposure to ≥1.0 µg/L of diflubenzuron; biomass was apparently unaffected at all treatment levels. Throughout the equilibration and treatment periods, all streams were qualitatively similar; *Pseudomonas* (0.38) and *Flavobacteria* (0.33) were most abundant, *Acinetobacter* (0.07), *Aeromonas* (0.06), and *Azotobacter* (0.05) were common, but less abundant. During the last treatment month, the streams contained ≥1.0 µg/L and experienced shifts in the relative abundances of the

TABLE 6. Water quality characteristics — monthly averages (SD)

Month	T (°C)	pH	D.O. (mg/L)	Hardness (mg/L as $CaCO_3$ equiv.)	Alkalinity (mg/L as $CaCO_3$)	$NO_3^- - NO_2^-$ (mg/L)	NH_3 (mg/L)	Total N (mg/L)	Total $PO_4^{=}$ (mg/L)	$O-PO_4^{=}$ (mg/L)
Sept.	14.2	7.0	9.9	28.5	2.4	0.148	0.005	0.057	0.111	0.051
	(1.0)	(0.2)	(0.2)	(9.0)	(0.1)	(0.011)	(0.003)	(0.047)	(0.015)	(0.002)
Oct.	13.0	7.0	10.3	26.0	2.5	0.080	0.007	0.040	.087	0.030
	(1.3)	(0.1)	(0.2)	(3.8)	(0.1)	(0.019)	(0.004)	(0.037)	(0.005)	(0.006)
Nov.	12.8	6.9	10.5	25.3	2.3					
	(1.7)	(0.1)	(0.6)	(5.6)	(0.2)					
Dec.	11.2	7.2	11.2	39.0	3.2	0.359	0.096	0.016	0.074	0.029
	(1.2)	(0.2)	(1.2)	(15.1)	(1.0)	(0.024)	(0.015)	(0.026)	(0.094)	(0.005)
Jan.	10.2	7.1	11.3	48.5	3.5	0.066	0.030	0.115	0.085	0.036
	(0.9)	(0.1)	(0.4)	(23.0)	(1.6)	(0.007)	(0.013)	(0.025)	(0.012)	(0.003)
Feb.	10.8	7.1	10.9	57.5	4.6					
	(0.6)	(0.1)	(0.3)	(4.4)	(0.4)					
Mar.	11.2	7.2	10.8	60.8	4.9	0.510	0.028	0.234	0.081	0.014
	(0.8)	(0.0)	(0.3)	(19.7)	(0.5)	(0.180)	(0.033)	(0.261)	(0.185)	(0.002)
Apr.	12.0	7.2	10.5	41.8	3.6	0.503	0.014	0.131	0.035	0.027
	(0.9)	(0.0)	(0.2)	(6.0)	(0.4)	(0.008)	(0.017)	(0.056)	(0.010)	(0.007)

TABLE 7. Measured concentrations (μg/L) of diflubenzuron in each stream channel, presented as monthly means ± SE.

Nominal Concn. (μg/L)	Measured mean concentrations (μg/L) ± SD				
	Dec.	Jan.	Feb.	March	April
0	<0.5	<0.5	<0.5	<0.5	<0.5
0	<0.5	<0.5	<0.5	<0.5	<0.5
0.1	<0.5	<0.5	<0.5	<0.5	<0.5
0.1	<0.5	<0.5	<0.5	<0.5	<0.5
1.0	0.95±0.07	0.93±0.15	1.05±0.21	0.84±0.15	0.89±0.02
1.0	1.07±0.05	1.10±0.04	1.02±0.02	0.81±0.09	0.83±0.09
10.0	10.51±0.78	9.06±1.30	11.28±1.33	9.51±0.98	10.49±0.84
10.0	9.47±0.70	9.80±0.47	12.65±0.65	9.03±0.89	10.50±0.91
50.0	49.38±6.46	59.25 (8.17)	59.67±18.12	79.0±14.07	90.0±5.48
50.0	55.13±6.35	61.75±7.85	56.0±16.31	83.05±10.83	92.33±5.79

dominant species; *Pseudomonas* (0.83) increased and *Flavobacteria* (0.10) and *Acinetobacter* (0.01) decreased. These alterations reduced species evenness and, therefore, reduced diversity. Because these alterations were observed at the conclusion of this study, their permanence could not be determined.

The results relating to the fungal decomposer functional group were inconclusive. Reductions in diversity and elevations in biomass (Fig. 9) were apparently associated with exposure to ≥1.0 μg/L of diflubenzuron. However, these effects were transient and variable in nature, lasting only a couple of months and showing no clear dose–response relationship. Also, because no fungal determinations were available until the start of diflubenzuron addition, pretreatment equivalence between streams could only be assumed.

STREAM CHEMISTRY

The water quality characteristics of the stream channels (Tables 6 and 7) are recorded as monthly mean values. For physical and inorganic parameters (Table 6), no statistically significant differences were apparent between any of the stream channels. Therefore, these parameters are reported as averages over all channels. The diflubenzuron concentrations (Table 7) purposely differ between treatment levels and are reported as monthly averages for each of the stream channels. Actual concentrations in the 0.1-μg/L treatment level and the control streams are not reported because the detection limit of the analytical method was 0.5 μg/L.

Discussion

The results of this study indicate that a standard set of single-species toxicity tests were adequate to predict the concentrations of the insecticide diflubenzuron that affected the structure and function of these complex laboratory stream communities. The calculated final chronic toxicity value of 0.06 μg/L is approximately an order of magnitude lower than

the minimum toxicant concentrations that affected the biomass and/or diversity of all stream functional groups.

This correspondence supports the assumption that the standard set of test species is representative of the range of sensitivities found in natural assemblages of species, at least at the genus level. Because the identification of many stream organisms could not be made to the species level, a critical test of the relative sensitivities of all species could not be made. Nevertheless, for all cases in which species identifications were available, no underprotected species were found.

Our study also indicates that the single-species tests did not predict the exact nature of all the effects observed in the stream communities. Effects which resulted from direct lethality to constituent species were well predicted. For example, reductions in the diversity and biomass of the invertebrate functional groups were fully expected, as a result of the high sensitivity of insects and crustaceans in the single-species tests. However, effects which resulted from altered interspecies interactions could not be predicted, without a priori knowledge of the trophic dynamics of the system. For example, the observed alterations in the biomass and diversity of the algal functional group were not expected; diflubenzuron produced no effect in the *Selenastrum* single-species test. The increase in algal biomass was an indirect effect, probably as a result of decreased predation by the impacted invertebrate herbivores. The subsequent decrease in algal diversity was apparently the result of increased competition for limited attachment sites among the enlarged algal populations. The best competitors under crowded conditions have been shown to be *M. varians* and *Synedra* sp. (Patrick 1977), and it was these populations which increased at the expense of less-adapted species. Without the knowledge that primary producers were initially herbivore limited and that release from this herbivore control would produce competition for space, these changes could not be accurately forecast.

This lack of correspondence between expected and observed community responses casts doubt upon the assumption that interactions need not be considered as a result of their relative unimportance or insensitivity. Apparent alterations in predator–prey and competition interactions produced significant shifts in the structure of the algal functional group. These interaction effects were approximately as sensitive as the direct lethal effects observed in the invertebrate functional groups, being exhibited at the 1.0-μg/L level.

The conclusions we draw from this study are probably conservative. Because of the limited duration of the study and the relative simplicity of these laboratory stream communities in relation to natural communities, the likelihood of finding differences between the single-species predictions and the community level responses should be minimized. These stream microcosms have a finite lifetime of ~8 mo, and only effects which appear within that time frame can be assessed. For many important stream organisms, this time period represents only a portion of one generation. Therefore, neither reproductive effects nor long-term interaction effects, which may take several generations to become apparent, can be evaluated. These stream microcosms are physically nearly homogeneous and, consequently, have less-diverse community structure than is found in natural systems. Therefore, some very sensitive species and/or interactions may be missing, and the effects on them will not be assessed.

A determination of the generality of these results will require additional research using a variety of chemicals and community types. Because of differences in modes of action and degrees of specificity, various classes of toxicants when added to the same community may differentially affect groups of species and types of interactions. As a result of differences in species composition and the relative importance that interactions play in community structure, various community types may respond differently to the same toxic substance. An overall assessment of many community types and toxicant classes will be necessary to establish the robustness of the assumptions underlying the use of single-species toxicity testing. This is one such study.

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ANDROS, J. D., AND R. R. GARTON. 1980. Acute lethality of copper, cadmium, and zinc to northern squawfish. Trans. Am. Fish. Soc. 109: 235–238.

ASTM. 1980. Standard E 72980. Practice for conducting acute toxicity tests with fishes, macroinvertebrates and amphibians. American Society for Testing and Materials, 1916 Race Street, Philadelphia, PA 19103, USA.

BUCHANAN, F. E., AND N. E. GIBBONS. 1974. Bergey's Manual of determinative bacteriology, 8th ed. Williams and Wilkins Company, Baltimore, MD. 1268 p.

CAIRNS, J. 1980. Beyond single species toxicity testing. Mar. Environ. Res. 3: 157–159.

COMMONWEALTH MYCOLOGICAL INSTITUTE. 1968. Plant pathologist's pocketbook. Commonwealth Mycological Institute, Kew, England. 267 p.

CORLEY, C., R. W. MILLER, AND K. R. HILL. 1974. Determination of N(4-chlorophenyl)-*N'*(2,6-diflurobenzoyl)-urea milk by high speed liquid chromatography. J. Assoc. Off. Anal. Chem. 57: 1269–1271.

EISELE, P. J., AND R. HARTUNG. 1976. The effects of methoxychlor on riffle invertebrate populations and communities. Trans. Am. Fish. Soc. 105: 628–633.

GARTON, R. R. 1980. A simple continuous-flow toxicant delivery system. Water Res. 14: 227–230.

GECKLER, J. R., W. B. HORNING, T. M. NEIHEISEL, Q. H. PICKERING, AND E. L. ROBINSON. 1976. Validity of laboratory tests for predicting copper toxicity in streams. Ecol. Res. Ser., U.S. Environ. Prot. Agency, EPA-600/3-76-116. Duluth, MN.

GIBSON, J. R. 1981. Safety margins: classical mammalian approaches and practical aspects of their present use in aquatic toxicology, p. 10–13. *In* D. R. Branson and K. L. Dickson [ed.] Fourth Conference on Aquatic Toxicology and Hazard Assessment, ASTM STP737. Am. Soc. Test. Mater. Proc.

HEATH, R. T. 1979. Holistic study of an aquatic microcosm: theoretical and practical implications. Intern. J. Environ. Stud. 13: 87–93.

HITCHOCK, S. W. 1965. Field and laboratory studies of DDT and aquatic insects. Conn. Agric. Exp. Stn. Bull. (New Haven) 668: 1–32.

INGOLD, C. T. 1942. Aquatic Hyphomycetes of decaying alder leaves. Trans. Brit. Mycol. Soc. 25: 339–417.

INGOLD, C. T., AND V. J. COX. 1957. *Heliscus stellatus sp. nov.* an aquatic hyphomycete. Trans. Brit. Mycol. Soc. 40: 155–158.

MERRITT, R. W., AND K. W. CUMMINS. 1978. An introduction to the aquatic insects of North America. Kendall/Hunt Publishing Company, Dubuque, IA. 441 p.

MOUNT, D. I. 1979. Adequacy of laboratory data for protecting aquatic communities, p. 112–118. *In* K. L. Dickson, A. W. Maki, and J. Cairns [ed.] Analyzing the Hazard Evaluation Process. Am. Fish. Soc.

1981. Margins of safety for aquatic communities, p. 5–9. *In* D. R. Branson and K. L. Dickson [ed.] Fourth Conference on Aquatic Toxicology and Hazard Assessment, ASTM STP737. Am. Soc. Test. Mater. Proc.

N.R.C. 1981. Testing for effects of chemicals on ecosystems: a report by the committee to review methods for ecotoxicity. National Academy Press, Washington, DC.

NEBEKER, A. V. 1973. Temperature requirements and life cycle of the midge *Tanytarsus dissimilis* (Diptera: Chironomidae). J. Kansas Entomol. Soc. 46: 160–165.

OEHLER, D. D., AND G. M. HOLMAN. 1975. Residue determination of Thompson-Hayward 6040 in bovine manure by high performance liquid chromatography. J. Agric. Food Chem. 23: 590–591.

PATRICK, R. 1977. Ecology of freshwater diatoms and diatom communities, p. 234–242. *In* D. Werner [ed.] The biology of diatoms. Botanical monographs, Vol. 13. Blackwell Scientific Publications, Oxford, England.

PETERSEN, R. H. 1962. Aquatic Hyphomycetes from North America. I. Aleurisoporae (Part I), and key to the genera. Mycologia 54: 117–151.

1963a. Aquatic Hyphomycetes from North America II. Aleurisporae (Part II), and Blastosporae. Mycologia 55: 18–29.

1963b. Aquatic Hyphomycetes from North America. III. Phialosporae and miscellaneous species. Mycologia 55: 570–581.

RANZONI, F. V. 1953. The aquatic Hyphomycetes of California. Farlowia 4: 353–398.

REISA, J. J. 1981. Margins of safety in the assessment of aquatic hazards of chemicals — some regulatory viewpoints, p. 15–27. *In* D. R. Branson and K. L. Dickson [ed.] Fourth Conference on Aquatic Toxicology and Hazard Assessment: ASTM STP737. Am. Soc. Test. Mater. Proc.

SAMUELSON, D. F. 1976. Water quality: western fish toxicology station and western Oregon rivers. Ecol. Res. Ser., U.S. Environ. Prot. Agency, EPA-600/3-76-077, Duluth, MN.

SHAYEGANI, M., A. M. LEE, AND L. M. PARSON. 1976. A scheme for the identification of non-fermentative gram-negative bacteria. Health Lab. Sci. 14: 83–90.

STEELE, M. B. 1979. Identification of non-fermentative Gram-negative bacilli by conventional biochemicals and dichotomous scheme. Wilmington Medical Center, Delaware Division Microbiology, Wilmington, DE.

STEELE, R., AND J. H. TORRIE. 1960. Principles and procedures of statistics: with special reference to the biological sciences. McGraw-Hill Book Company, Inc. New York, NY. 481 p.

U.S.E.P.A. 1975. Methods for acute toxicity tests with fish, macroinvertebrates, and amphibians. Ecol. Res. Ser., U.S. Environ. Prot. Agency, EPA-660/3-75-009, Corvallis, OR.

Methods for ecological toxicology: a critical review of laboratory multispecies tests. Office of Toxic Substances, U.S. Environ. Prot. Agency, EPA-560/11-80-026, Washington, DC.

WEBER, C.I. 1973. Biological field and laboratory methods for measuring the quality of surface waters and effluents. Environ. Monit. Ser., U.S. Environ. Prot. Agency, EPA-670/4-73-001, Cincinnati, OH.

WEISS, C. M. 1976. Field evaluation of the algal assay procedure on surface waters of North Carolina, p. 29–76. *In* E. J. Middlebrooks, D. H. Falkenborg, and T. E. Maloney [ed.] Biostimulation and nutrient assessment, Ann Arbor Science, Ann Arbor, MI.

WILLIAMS, D. A. 1972. The comparison of several dose levels with a zero dose control. Biometrics 28: 519–531.

Appendix

1. Invertebrate scrapers
   - Emphemeroptera
     Baetis, Epeorus, Cinygmula, Rithrogena, Paraleptophlebia, Ephemerella, Stenoma
   - Plecoptera
     Pteronarcella, Brachyptera, Paraperla
   - Tricoptera
     Neophylax, Glossosoma, Dicosmoecus, Anagapetus, Leptoceridae, Hesperophylax, Ecclisomyia
   - Diptera
     Pericoma, Blepharicera
   - Coleoptera
     Optioservus, Cleptelmis, Zaitzevia, Heterlimnius, Narpus, Ampumixis
   - Mollusca
     Juga plicifera

2. Invertebrate shredders
   - Ephemeroptera
     Paraleptophlebia, Ephemerella
   - Plecoptera
     Pteronarcys, Pteronarcella, Nemoura, Leuctra, Peltoperla, Capnia
   - Tricoptera
     Onocosmoecus, Hydatophylax, Micrasema, Lepidostoma, Hesperophylax
   - Diptera
     Tipula
   - Coleoptera
     Lara

3. Invertebrate collectors–gatherers–filterers
   - Ephemeroptera
     Ameletus, Baetis, Epeorus, Cinygmula, Rithrogena, Paraleptophlebia, Ephemerella, Stenonema
   - Plecoptera
     Isoperla, Alloperla, Peltoperla
   - Tricoptera
     Hydatophylax, Wormaldia, Hydropsyche, Polycentropus, Micrasema, Hesperophylax, Ecclisomyia
   - Diptera
     Antocha, Prosimulium, Simulium, Pericoma, Dixa, Tipula, Chironomini, Tanytarsini, Corynoneurini, Orthocladini
   - Coleoptera
     Optioseruus, Oreodytes, Zaitzevia, Heterlimnius, Narpus, Ampumixis
   - Miscellaneous
     Ostracoda, Copepoda, Cladocera, Oligochaeta, Nematoda

4. Invertebrate predators
   - Plecoptera

Pteronarcella, Acroneuria, Hesperoperla, Isoperla, Alloperla, Isogenus, Paraperla

Tricoptera

Rhyacophila, Polycentropus

Diptera

Bessia, Hemerodromia, Pedicia

Pentaneurini, Ceratopogoninae, Empididae, Tanypodini, Tabanidae

Coleoptera

Oreodytes, Hydroporous

Carabidae

Odonata

Octogomphus

Miscellaneous

Scalis (neuroptera), Hydracuriana (mite)

Hydrozoa

5. Algal primary producers

Achnanthes lanceolata, Navicula sp., *Cocconeis placentula, Nitzschia* sp., *Gomphonema acuminatum* var. *coronata, Rhoicosphenia curvata, Melosira varians, Synedra* sp., *Meridion circulare, Surirella* sp., *Fragilaria* sp., *Cymbella minuta, Cymbella sinuata, Cyclotella* sp., *Frustulia rhomboides, Epithemia turgidida* var. *Westermanni, Hantzschia* sp., *Eunotia arcus, Pinnularia subcapitata* var. *pavaststriata, Pinnularia mesolepta* var. *mesolepta*

6. Fungal decomposers

Heliscus stellatus, Articulospora tetracladia, Tetrachaetum elegantus, Heliscus longibranchus, Clavariopsis aquatica, Lunulospora curvula, Anguillospora pseudolongissma, Tetracladium marchalianum

7. Bacterial decomposers

Pseudomonas, Flavobacteria, Acinetobacter, Aeromonas, Azotobacter, Enterobacter, Moraxella, Micrococcus, Lactobacillus, Alcaligenes, Xanothomonas, Beijerinckia, Azomonas, Vibrio Beggiatoaceae

Elemental Composition of Bone from White Sucker (*Catostomus commersoni*) in Relation to Lake Acidification

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FRASER, G. A., AND H. H. HARVEY. 1982. Elemental composition of bone from white sucker (*Catostomus commersoni*) in relation to lake acidification. Can. J. Fish. Aquat. Sci. 39: 1289–1296.

Bone was decalcified in fish from three acid lakes and manganese was increased greatly in bone of fish from the most acid lake. The mean centrum calcium content of white suckers (*Catostomus commersoni*) captured in George Lake (pH 4.65) was 16% lower than in white suckers from three lakes with near-neutral pH levels. In two other acid lakes, King (pH 5.08) and Crosson (pH 5.36), centrum calcium was reduced significantly in white suckers. Centrum manganese was elevated fivefold in white sucker from recently acidified George Lake, and tended to be elevated in this species from King Lake. White suckers from George Lake exhibited shorter caudal vertebrae and some of these fish had deformed caudal fins. These anomalies may be indicative of bone demineralization. All of the study lakes were located in south-central Ontario, including the La Cloche Mountains, North Bay, Algonquin, Haliburton, and Muskoka.

Key words: lake acidification, bone composition, calcium, manganese, white sucker

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Chez des poissons provenant de trois lacs acides, il y a décalcification des os, alors que dans le lac le plus acide, la teneur des os en manganèse est de beaucoup plus élevée. Le contenu moyen de calcium dans le centrum de meuniers noirs (*Catostomus commersoni*) capturés dans le lac George (pH 4,65) est de 16 % inférieur à celui de poissons de la même espèce habitant trois lacs à pH se rapprochant du point neutre. Dans deux autres lacs acides, les lacs King (pH 5,08) et Crosson (pH 5,36), le centrum contient nettement moins de calcium. Le manganèse du centrum est de cinq fois plus élevé chez des meuniers noirs du lac George, récemment acidifié, et tend a être élevé chez des individus du lac King. Les meuniers noirs du lac George possèdent des vertèbres caudales plus courtes, et certains exhibent des difformités à la nageoire caudale. Ces anomalies peuvent indiquer une déminéralisation des os. Tous les lacs étudiés sont situés dans le centre-sud de l'Ontario, y compris les régions des montagnes La Cloche, North Bay, Algonquin, Haliburton et Muskoka.

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THE phenomenon of the acidification of freshwaters resulting from acid precipitation has been reported to be of both regional and widespread occurrence in Europe (Odén and Ahl 1970; Braekke 1976; Overrein et al. 1980) and eastern North America (Likens 1976; Dillon et al. 1978; Harvey et al. 1981). In such acidified lakes and rivers, partial or complete loss of fish populations is well documented (Jensen and Snekvik 1972; Beamish and Harvey 1972; Almer et al. 1974; Schofield 1976; Sevaldrud and Muniz 1980). Despite such large-scale losses, the mechanisms which caused these reductions are understood only in part. The commonest cause of extinction appears to be failed recruitment of new age-classes (Ryan and Harvey 1980; Rosseland et al. 1980), brought about by reduced egg and larval survival (Schofield 1976), failed maturation (Mount 1973; Craig and Baksi 1977), or reduced spawning success (Beamish et al. 1975). Older fishes also are lost from populations of white sucker (*Catostomus commersoni*) (Harvey 1980) and brown trout (*Salmo trutta*) (Rosseland et al. 1980). The present investigation is limited to acid stress and metal stress in adult fish.

In acid-stressed fishes, ionoregulation failure has been indicated by reduced chloride and sodium in plasma and muscle (Fromm 1980; Muniz and Leivestad 1980; Spry et al. 1981). In water of low pH, Na^+ uptake at the gill is reduced and Na^+ efflux is increased (Packer and Dunson 1970; McWilliams and Potts 1978). Demineralization of bone could release appreciable amounts of Na^+ to regulate plasma concentra-

[1]For monovalent ions 1 meq = 1 mmol; for divalent ions such as calcium, magnesium, and manganese 1 meq = 2 mmol.

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TABLE 1. Location and morphometry of the six study lakes.

Lake	Lat.	Long.	Mean depth (m)	Max. depth (m)	Area (ha)	Volume ($m^3 \times 10^6$)
Blue Chalk	45°12′	78°56′	8.5	23.0	49.4	4.21
Crosson	45°05′	79°02′	8.4	25.0	56.8	4.77
George	46°02′	81°24′	18.6	36.6	147.9	27.53
Harp	45°23′	79°07′	12.4	40.0	66.9	8.26
King	45°53′	79°30′	2.6	5.8	29.1	0.75
Opeongo	45°42′	78°23′	12.7	47.0	5894.0	745.63

tions. This may have been the cause of the increased plasma $[Na^+]$ following acid exposure in experiments conducted by Holeton et al. (1982).

Calcium regulation may also be affected in fishes in acid water. Beamish et al. (1975) reported a high frequency of spinal deformities among white suckers in George Lake and hypothesized that this could be a consequence of bone decalcification. These workers postulated that chronic acidosis in fish could result in blood pH being maintained by demineralization of bone, with 1 mol of tricalcium phosphate making possible the excretion of 4 mol of acid (White et al. 1978). However, there is very limited evidence to support the hypothesis that fish could buffer, even temporarily, incoming acid via mobilization of bone salts with the excretion of the released Ca^{2+}. Rainbow trout (*Salmo gairdneri*) exposed to pH 4 lost Ca^{2+} at a rate of 7.25 μmol $Ca^{2+} \cdot kg^{-1} \cdot h^{-1}$ (Holeton et al. 1982), but plasma $[Ca^{2+}]$ does not appear to change in rainbow trout held at low pH (Neville 1979; McDonald et al. 1980). G. F. Holeton (unpublished data) suggested that such losses of Ca^{2+} may have been necessary to maintain extracellular $[Ca^{2+}]$. McDonald and Wood (1981) reported increased renal excretion of calcium and phosphate in acid-stressed rainbow trout.

Mammals have been shown to regulate hydrogen ion levels through the dissolution of major mineral components of bone ($Ca_3(PO_4)_2$ and $CaCO_3$). It was shown by Irving and Chute (1932) that ingested acid was neutralized in part by carbonates derived from bone in the rat. Lehmann et al. (1965) suggested that bone demineralization could supply additional buffer in chronic metabolic acidosis in man. Based on "unaccounted for" calcium, Lehmann et al. (1966) concluded that bone was the only source of the large amount of calcium in acidosis, but additional losses of phosphorus could have come from other tissues. Mobilization of bone carbonate, calcium, and phosphorus during acidosis in the dog was demonstrated by Burnell and Teubner (1971).

In acidified freshwaters, metal levels are also elevated in water, and may present additional physiological stress to fishes. The death of fishes in acid waters has been linked to the accumulation of aluminum on gill surfaces (Schofield and Trojnar 1980; Muniz and Leivestad 1980). Aluminum levels are elevated in acidified waters (Schofield 1976; Wright and Henriksen 1978; Dickson 1978) as a result of strong acids of atmospheric origin reacting with aluminum-containing minerals in soils (Johnson 1979). This elevated aluminum can exist in several forms, differing in toxicity to fishes (Driscoll et al. 1980). Several other metals are elevated in acidified waters: cadmium (Dickson 1975), nickel (Beamish and Van Loon 1977), zinc and lead (Henriksen and Wright 1978), and mercury (Almer et al. 1978; Wood 1980). Correlations have been reported between the mercury content of fishes and water pH in pike (*Esox lucius*) (Hultberg 1977a) and yellow perch (*Perca flavescens*) (Suns et al. 1980). The mercury content of walleye (*Stizostedion vitreum*) was greater from soft-water lakes than from lakes of higher alkalinity (Scheider et al. 1979).

Manganese also has been reported to be increased greatly in concentration in acidified lakes in Sweden (Dickson 1975), parts of Norway (Wright et al. 1977), and Ontario (Beamish et al. 1975; Somers 1980; Harvey and Lee 1980; Ontario Ministry of Environment, unpublished data). This was attributed again to the leaching of soils by acid rain, but in addition, Schindler et al. (1980) demonstrated the recruitment of manganese from lake sediments during the experimental acidification of a lake. The effect of this manganese on fishes is not known. A threefold increase in the manganese content of white sucker scales for fish captured in acid George Lake was reported by Lockhart and Lutz (1977). These workers postulated that elevated levels of manganese could interfere with calcium metabolism. However, toxicity studies have reported that manganese is relatively nontoxic to fishes. In Water Quality Criteria (1972) it was suggested that a concentration of 0.1 mg/L manganese may constitute a hazard, but that 0.02 mg/L involved minimal risk. Little testing has been done on manganese toxicity at low pH.

The purpose of this study was twofold. First, to measure the mineral content of bone from fish captured in acid and near-neutral lakes. Second, this study endeavored to determine the manganese content of hard tissues in white suckers, and relate it to manganese concentration in water and lake acidification.

Materials and Methods

Calcium and manganese content was determined in ribs, trunk centra, caudal centra, hypurals, and opercula of white suckers from George Lake origin, by neutron activation analysis (Kruger 1971; DeSoete et al. 1972).

Six lakes were chosen for more intensive sampling on the basis of lake morphometry (Table 1), water chemistry (Table 2), and on the basis of past experience with fish populations in these lakes (Harvey 1981). Three of the six lakes were acid, based on the Swedish criterion that an acid lake has a pH of less than 5.5 (Anon. 1979). The three control lakes were near neutral in pH, with values ranging from pH 6.4 to 6.6.

One hundred and nineteen white suckers captured in the six

TABLE 2. Mean value and range of selected water chemistry variables in the six study lakes.[a] The number of determinations is shown in parentheses adjacent to the mean if less than three, otherwise three or more determinations.

Lake	Mean pH at 2–3 m	T.I.P.[b] alkalinity (μeq/L)	Conductivity (μS/cm)	Concentration (mg/L)				Concentration (μg/L)	
				DOC[c]	Ca	Na	SO_4	Mn	Al
George	4.61	−10.2	31	1.5	3.0	0.8	11.9	137	190(1)
(1979)	(4.56–4.69)	(−25.2–0.3)	(9–42)	(1.4–1.6)	(2.8–3.4)	(0.7–0.9)	(11.5–12.0)	(130–142)	
	4.70	−3.2	42	1.4	2.7	0.8	11.5(2)	148	180(2)
(1980)	(4.64–4.75)	(−20.2–8.1)	(30–49)	(1.3–1.4)	(2.2–3.0)	(0.7–1.0)		(142–160)	(160–190)
King	5.08	−3.5	26	5.6(2)	2.8	0.8	9.3	93	90(1)
(1979)	(4.96–5.25)	(−5.9–0.3)	(8–35)	(5.4–5.8)	(2.6–3.0)	(0.7–0.8)	(9.0–9.5)	(85–108)	
Crosson	5.36(2)	0.3	27	4.0	2.5	0.8	8.5	28	50(1)
(1979)	(5.26–5.49)	(−9.4–7.7)	(15–33)	(3.9–4.2)	(2.4–2.8)	(0.7–0.9)	(8.0–9.0)	(16–40)	
Opeongo[d]	6.37	69.0(2)	35	4.7	3.5	1.2	10.3	10(2)	20(2)
(1978–79)	(6.29–6.45)	(66.2–71.9)	(30–44)	(4.4–4.9)	(3.4–3.6)	(1.1–1.3)	(9.5–11.5)	(6–13)	
Harp	6.45	116.0[e]	36	4.5	3.4	1.0	9.5	28(1)	50(1)
(1979)	(6.25–6.83)	(100–120)	(34–42)	(4.2–5.0)	(3.2–3.4)	(0.9–1.2)	(9.0–10.0)		
Blue Chalk	6.59	64.1	27(2)	1.8	2.9	0.9	7.1	24	50(1)
(1980)	(6.46–6.74)	(62.4–68.4)	(23–30)	(1.7–2.0)	(2.4–3.4)	(0.7–1.1)	(6.5–7.5)	(20–28)	

[a]Alkalinity, pH, and conductivity in lakes George, King, Crosson, and Opeongo were measured by the Lake Ecosystem Working Group, University of Toronto; all other chemical analyses were performed by Ontario Ministry of Environment.
[b]T.I.P. = total inflection point alkalinity.
[c]DOC = dissolved organic carbon.
[d]Water chemistry data not available for 1980.
[e]Measured as total fixed end-point alkalinity (TFEP) at pH 4.5.

lakes during 1979 and 1980 were sampled for weight, length, sex, and maturity, plus fin-ray and scale samples were taken for age determination. Caudal vertebrae were taken immediately dorsal to the posterior base of the anal fin (approximately caudal vertebrae #9–13); spines, arches, and other attached tissues were removed from the vertebrae leaving only the centra. Centra were dried in polythene irradiation vials at 60°C to constant weight. Centra lengths were measured as described by Komada (1980) using Kanon calipers (reading error = ±0.02 mm). The relative standard deviation associated with the measure of centra size was 1.1%. Sufficient centra were selected so that at least 0.1 g of bone could be analyzed by neutron activation analysis for calcium, manganese, sodium, magnesium, and chloride.

All samples analyzed using neutron activation analysis were irradiated for 2 min with a neutron flux $2 \times 10^{11}/cm^2$ using SLOWPOKE-1 reactor, University of Toronto (Hancock 1976). After a 1-min delay, materials were counted for 5 min using one of two gamma spectrometry systems (Canberra Ge(Li) detector; model 7600 cryostat; 452 Ortec spectroscopy amplifier; 8100 series, 4096 channel Canberra analyzer; teletype printer). Gamma-ray peak intensities were determined by automatic analyzer integration of manually selected spectral regions of interest at or near each peak. Teletype output integrals were then analyzed to determine elemental concentrations using a Fortran IV program (Nolan 1971). Element standards were prepared and verified with a second standard. Standards were compared with those calculated by R. G. V. Hancock (University of Toronto, unpublished data) for Analyzer 1 to establish experimental accuracy. Standard values stated by Hancock were evaluated at a time delay of 0 min and converted to a 1-min delay according to Kruger (1971). All six standards determined by Hancock were within 5% of those used here, except sodium (8.6%) and magnesium (12.8%). Relative precision associated with these analyses was estimated by evaluating duplicate samples from six fish. The calculated average relative deviations (Christian 1971) for each element were as follows: calcium, 2.4%; manganese, 4.0%; sodium, 3.4%; magnesium, 6.5%; and chloride, 3.9%.

Most white suckers that appeared to be deformed were X-rayed with either a Hewlett-Packard 43805N X-Ray System Faxitron Series (35 kilovoltage peak; 3.5 min), or a General Electric DXS-350 X-ray unit (45 kVp; 100 milliampere, 1.50 s), using Kodak Industrex AA5 film.

Unless indicated otherwise, all analyses were computed using the Statistical Analysis System (SAS) (Helwig and Council 1979).

Results

The scan of five bony tissues from white suckers yielded considerable variation in calcium and manganese content (Table 3). Comparison of element means for each bone type revealed the following: ribs and opercula showed high calcium and high manganese; hypurals showed the lowest calcium plus high manganese; trunk and caudal centra exhibited low calcium and lowest manganese levels.

TABLE 3. Mean[a] (± SE) elemental composition of bone in white sucker from George Lake.

Element	Ribs	Opercula	Hypurals	Trunk centra	Caudal centra
	meq/100 g dry weight				
Ca	1085±33	1091±28	733±35	831±12	817±28
Mn	1.97±0.18	2.00±0.22	2.04±0.36	1.57±0.18	1.64±0.15

[a]Five fish with a mean fork length 39.1 ± 1.6 cm were analyzed, except for hypural bones, where the sample was three fish.

TABLE 4. Mean (± SE) elemental composition of centra from white suckers captured in six lakes 1979–80. If the sample size is different from *n*, it is in parentheses adjacent to the mean. Means for a given measure that do not contain the same letter superscript are significantly different ($\alpha = 0.05$, Duncan's test).

Lake	pH	*n*	Fork length (cm)	Wet weight (g)	Concentration (meq/100 g dry weight)				
					Ca	Mn	Mg	Na	Cl
George	4.65	20	32±2	522±72	944 ± 22^{c}	2.42 ± 0.15^{a}	29 ± 2^{c}	13.0 ± 0.4^{d}	4.4 ± 0.3^{b}
King	5.08	16	27±1	266±12	1049 ± 14^{b}	0.70 ± 0.05^{b}	34 ± 1^{ab}	$15.4\pm0.3(8)^{abc}$	6.0 ± 0.5^{a}
Crosson	5.36	17	31±2	464±83	1096 ± 16^{b}	0.32 ± 0.02^{c}	37 ± 2^{ab}	14.2 ± 0.6^{cd}	3.9 ± 0.3^{b}
Opeongo	6.37	20	39±1	857±44(18)	1129 ± 10^{a}	0.35 ± 0.02^{c}	34 ± 1^{b}	16.1 ± 0.3^{ab}	4.5 ± 0.2^{b}
Harp	6.45	19	33±1	430±28	1121 ± 14^{a}	0.39 ± 0.02^{c}	38 ± 1^{a}	14.8 ± 0.3^{bc}	4.5 ± 0.2^{b}
Blue Chalk	6.59	27	38±1	759±39	1111 ± 13^{a}	0.59 ± 0.05^{b}	$33\pm1(26)^{b}$	16.8 ± 0.5^{a}	5.2 ± 0.3^{a}

Mean concentrations are reported for calcium, manganese, sodium, chloride, and magnesium in centra of white suckers from the six lakes (Table 4). Data from five George Lake white suckers captured in 1979 were combined with 1980 data from 15 fish because mean concentrations for each element did not differ significantly between years ($P \geq 0.03$, *t*-test). Similarly, centra concentrations for different sexes within a given lake were combined because no significant differences existed ($P \geq 0.03$, *t*-test).

Homogeneity of group variances was tested using Levene's test (BMDP, Brown and Dixon 1979) before computing one-way analyses of variance (ANOVA) between element means for fish from the six lakes (Table 4). These tests revealed no significant differences ($P > 0.1$) between lakes with respect to variances of four elements (manganese data were log transformed). However, centrum calcium variances differed significantly ($P < 0.01$) between lakes. Consequently, the latter ANOVA test must be evaluated with caution.

One-way analyses of variance revealed significant ($P < 0.01$) differences between lakes with respect to backbone concentrations for all five elements measured in fish. Duncan's multiple range tests ($\alpha = 0.05$) were used to determine where significant differences occurred between lakes for each element mean (Table 4). The mean centrum calcium content of George Lake fish was significantly lower than that of white suckers from the other five study lakes. Calcium was reduced 16% relative to the mean of 1118 meq/100 g dry weight[1] for 66 fish in the three circumneutral lakes (Opeongo, Harp, and Blue Chalk). Backbone calcium was also significantly lower in white suckers from lakes King and Crosson; however, respective concentrations were not significantly different from each other.

George Lake white suckers possessed the highest centra manganese concentrations, fivefold greater than the mean for fish from the three lakes at near-neutral pH levels. King Lake white suckers also had an elevated manganese level that differed significantly from all other fish except those from Blue Chalk Lake. No clear relationship was observed between manganese content of white sucker centra and total manganese in water.

George Lake white suckers exhibited large variations in both calcium and manganese content of centra (Fig. 1). Differences in fish size or sex did not contribute to this variability. Also, no correlation was found between age and calcium content of centra, or age and manganese content in white suckers from any lake. However, the range of ages available in any sample was too small to be confident that such a relationship did not exist. The ratio of centra calcium to manganese was approximately 300:1, and although manganese was elevated where calcium was decreased, manganese was not present in simple substitution for calcium.

Backbone sodium was reduced 18% in George Lake white suckers compared with suckers from the circumneutral lakes; this element also tended to be reduced in centra of Crosson Lake fish. Bone magnesium levels were significantly lower ($\alpha = 0.05$) in George Lake white suckers. Also, the lowest centra magnesium concentration (19 meq/100 g dry weight) was observed in centra of a George Lake sucker. Chloride concentrations in bone showed no pattern between lakes.

White sucker fork length was highly correlated with caudal centrum length (Fig. 2). At each fork length, centra lengths were compared between fish from the different lakes. At lower fork lengths (less than 36 cm), centra tended to be smaller in fish from the most acid environment, George Lake. However, at greater fish sizes, a few fish from lakes George and Crosson showed the opposite, with larger centra relative to fork length. The regression line for centrum length versus fork length was $Y = 0.60 + 0.104X$ for white suckers from

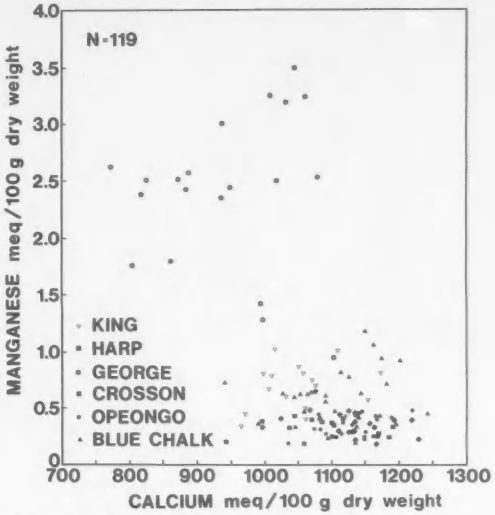

FIG. 1. Calcium versus manganese concentrations in centra of white suckers from three acid (George, King, Crosson) and three near-neutral (Harp, Opeongo, Blue Chalk) lakes in south-central Ontario.

five lakes, and $Y = -0.35 + 0.126X$ for George Lake fish (Fig. 2). Intercepts of these lines were significantly different ($P < 0.01$); however, the slopes were not significantly different ($P > 0.05$).

Bone deformities were observed in the tail region of some white suckers captured in George Lake. The most deformed fish, as determined by X rays, had the second lowest backbone calcium concentration (803 meq/100 g dry weight) of the 20 fish sampled from George Lake, 1979–80. The fish with the lowest calcium level (773 meq/100 g dry weight) was captured in 1980, and classified as deformed based on shape, but was not X-rayed. Bone manganese concentrations were not greater in white suckers with bone deformities.

Discussion

In this study, caudal centra of white suckers captured in George Lake showed a mean calcium concentration (944 meq/100 g dry weight) which was significantly lower than the mean for suckers from the three lakes with near-neutral pH levels (1118 meq/100 g dry weight). Also, the lengths of caudal centra tended to be shorter in some George Lake white suckers (less than 36 cm fork length) compared with white suckers from the control lakes. These observations are consistent with the X-ray findings of Beamish et al. (1975) in which some deformed fish showed malformed centra, and the suggestion that such fish could be demineralized.

Lockhart and Lutz (1977) measured the calcium content of anterior ribs collected from George Lake white suckers in 1972 (mean 1108 meq/100 g dry weight) and found no difference as compared with the calcium concentration (1118 meq/100 g dry weight) of suckers from (non-acid) Lake Manitoba. Their results are now more understandable following analyses of five types of bone in George Lake suckers. Ribs and opercula were not decalcified, whereas hypurals, trunk centra, and caudal centra exhibited lower calcium concentrations. It is possible that the calcium dynamics of white sucker ribs is unlike that of the vertebral column. Such variation in calcium dynamics between bony parts has been documented in mammals (Neuman and Neuman 1958).

Heretofore, a reduced concentration of calcium in bone has not been documented in acid-stressed fishes. This could have occurred if George Lake white suckers attempted to regulate extracellular hydrogen ion levels through the dissolution of major mineral components of bone. There has been no direct measurement of bone calcium loss from fishes under controlled acid conditions; however, increased renal excretion of calcium and phosphate in acid-stressed rainbow trout has been reported (McDonald and Wood 1981). Holeton et al. (1982) reported a net loss of Ca^{2+} from rainbow trout exposed to pH 4.0.

Low bone calcium levels in these fish could also have resulted from reduced deposition of calcium in bone during growth. Nelson (1982) reported that rainbow trout alevins subjected to pH 4.8 and 4.3 ($[Ca^{2+}] = 9.3$ mg/L) for more than 10 d exhibited a fewer number of ossified jaw teeth and branchiostegal rays relative to control fish. Nelson suggested that once calcium stores from the yolk sac were exhausted, alevins at low pH may have been unable to transport calcium from the environment, or the formation of calcium hydroxyapatite was inhibited. A decrease in active uptake of calcium from water at low pH was suggested by the enzyme work of Umehara and Oguri (1978) with goldfish (*Carassius auratus*). Hultberg (1977b) noted a reduction in otolith $CaCO_3$ deposition coinciding with acid exposure in young brown trout. Uptake of calcium has been reported in fish from both medium water and via dietary sources (Podoliak and Holden 1965; Fleming 1967); however, the relative importance of each is not known. Work with acid-exposed crayfish (Malley 1980) revealed an inhibition of calcium uptake below pH 5.75 and reduced calcification of the exoskeleton.

White suckers in George Lake exhibited a mean sodium concentration of 13 meq/100 g dry weight versus a mean of 16 meq/100 g dry weight in the centra of fish from the three control lakes, a significant reduction of 18%. Lockhart and Lutz (1977) found a mean sodium content of 17 meq/100 g dry weight in anterior ribs of George Lake fish, compared with 16 meq/100 g in suckers from Lake Manitoba. The results of the present study are consistent with the hypothesis that both sodium and calcium would be recruited from bone into extracellular fluids in acid-stressed fish. However, it remains possible that George Lake white suckers formed bone deficient in both calcium and sodium. Some 25–26% of bone sodium appears to be exchangeable in mammalian bone (Neuman and Neuman 1958). Chloride content of centra did not differ in fishes from acid and circumneutral lakes. Mammalian studies suggest that bone does not act as a reservoir for chloride ions (Neuman and Neuman 1958).

A reduction in ossified skeletal parts could be an important factor in fish loss from freshwaters at low pH. Low bone mineral levels could cause bone deformities like those observed in George Lake fish. Such deformations could

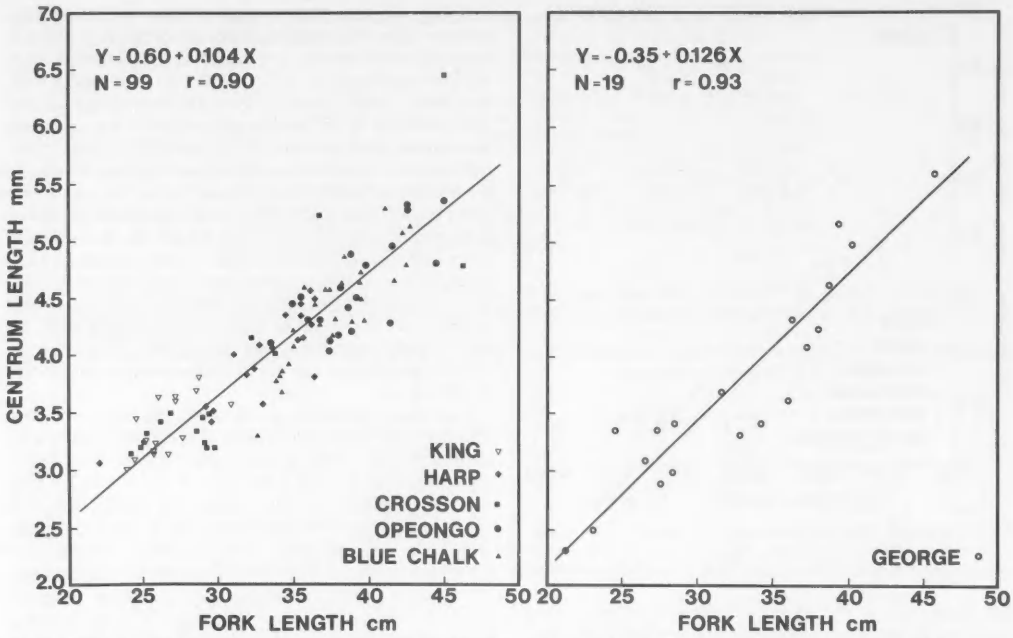

FIG. 2. Comparison of regressions of centrum length on fork length, for white sucker from five lakes and for George Lake fish. Intercepts differ significantly ($P < 0.01$).

make fish more susceptible to predation and environmental damage. Also, reduced calcium reserves may hinder normal ova formation.

George Lake white suckers showed a mean centrum manganese content of 2.42 meq/100 g dry weight, approximately fivefold greater than that found in white suckers from the three near-neutral lakes. Elevated manganese in bone of fishes from an acidified lake has never been reported. However, Lockhart and Lutz (1977) reported a threefold greater concentration of manganese in white sucker scales (2.01 meq/100 g dry weight) from George Lake in comparison with white sucker in non-acid Roddy Lake (0.58 meq/100 g).

No clear relationship was observed between the manganese concentration of white sucker centra and total manganese in lake water. This could result if manganese available to fish varies with chemical and physical factors in a lake. For example, manganese is known to form stable complexes with organic molecules (Wetzel 1975) and in that form may not be available for biological processes.

Manganese uptake, storage, excretion, and toxicity in fishes have received modest attention. Manganese is an essential metal required by fishes (Ogino and Yang 1980), and diet appears to constitute the major pathway for accumulation in marine fishes (Kimura and Ichikawa 1976; Pentreath 1976). However, recent work by Miller et al. (1980) suggests that largemouth bass in freshwater derive manganese from both food and water, with uptake affected by temperature but not dissolved oxygen. Manganese seems to be regulated at relatively constant tissue concentrations by adjusting elimination rates to equal uptake. In our study white suckers did not appear to accumulate manganese with increasing age, and this implies that bone manganese and water manganese were in steady state. Thus, it is possible that under conditions of elevated water manganese substantial metabolic energy may have to be expended to maintain relatively constant manganese concentrations (Cross et al. 1973), producing additional physiological stress in fishes already under acid stress. However, this manganese steady state could be achieved passively between fish and medium water. Manganese toxicity in fishes has not been studied adequately at chronic, sublethal levels, in acid water.

In humans, Chandra et al. (1974) suggested that manganese poisoning may alter calcium metabolism. However, it cannot be concluded that elevated manganese in bone of white suckers from George Lake was interfering with calcium metabolism, as it was not possible in this study to disaggregate the effects of acid stress from any direct effect of manganese. As yet, no explanation can be given for differences in calcium and manganese between centra and other bony tissues.

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ALMER, B., W. DICKSON, C. EKSTRÖM, AND E. HÖRNSTRÖM. 1978. Sulfur pollution and the aquatic ecosystem, p. 271–311. *In* J. O. Nriagu [ed.] Sulfur in the environment. Part II. Ecological impacts. J. Wiley and Sons, Inc., New York.

ALMER, B., W. DICKSON, C. EKSTRÖM, E. HÖRNSTRÖM, AND U. MILLER. 1974. Effects of acidification on Swedish lakes. Ambio 3: 30–36.

ANON. 1979. Kalkning av sjöar och vattendrag 1977–1979. Information från Sötvattenslaboratoriet, Drottningholm (8). 67 p.

BEAMISH, R. J., AND H. H. HARVEY. 1972. Acidification of the La Cloche Mountain Lakes, Ontario, and resulting fish mortalities. J. Fish. Res. Board Can. 29: 1131–1143.

BEAMISH, R. J., W. L. LOCKHART, J. C. VANLOON, AND H. H. HARVEY. 1975. Long-term acidification of a lake and resulting effects on fishes. Ambio 4: 98–102.

BEAMISH, R. J., AND J. C. VANLOON. 1977. Precipitation loading of acid and heavy metals to a small acid lake near Sudbury, Ontario. J. Fish. Res. Board Can. 34: 649–658.

BRAEKKE, F. H. [ed.] 1976. Impact of acid precipitation on forest and freshwater ecosystems in Norway. SNSF-project. Res. Rep. FR 6/76. 111 p.

BROWN, M. B., AND W. J. DIXON [ed.] 1979. BMDP-79. Biomedical Computer Programs P-Series. University of California Press, Berkeley. 880 p.

BURNELL, J. M., AND E. TEUBNER. 1971. Changes in bone sodium and carbonate in metabolic acidosis and alkalosis in the dog. J. Clin. Invest. 50: 327–331.

CHANDRA, S. V., P. K. SETH, AND J. K. MANKESHWAR. 1974. Manganese poisoning: clinical and biochemical observations. Environ. Res. 7: 374–380.

CHRISTIAN, G. D. 1971. Analytical chemistry. John Wiley Inc., New York. 508 p.

CRAIG, G. R., AND W. F. BAKSI. 1977. The effects of depressed pH on flagfish reproduction, growth and survival. Water Res. 11: 621–626.

CROSS, F. A., L. H. HARDY, N. Y. JONES, AND R. T. BARBER. 1973. Relationship between total body weight and concentrations of manganese, iron, copper, zinc, and mercury in white muscle of bluefish (*Pomatomus saltatrix*) and a bathyl-demersal fish *Antimora rostrata*. J. Fish. Res. Board Can. 30: 1287–1291.

DESOETE, D., R. GIJBELS, AND J. HOSTE. 1972. Neutron activation analysis. Wiley-Interscience, London. 836 p.

DICKSON, W. 1975. The acidification of Swedish lakes. Inst. Freshwater Res. Drottningholm. Rep. 54: 8–20.

1978. Some effects of acidification of Swedish lakes. Verh. Int. Verein. Limnol. 20: 851–856.

DILLON, P. J., D. S. JEFFRIES, W. SNYDER, R. REID, N. D. YAN, D. EVANS, J. MOSS, AND W. A. SCHEIDER. 1978. Acidic precipitation in south-central Ontario: recent observations. J. Fish. Res. Board Can. 35: 809–815.

DRISCOLL, C. T., J. P. BAKER, J. J. BISOGNI, AND C. L. SCHOFIELD. 1980. Aluminum speciation in dilute acidified waters and its effect on fish. Nature (London) 284: 161–164.

FLEMING, W. R. 1967. Calcium metabolism of teleosts. Am. Zool. 7: 835–842.

FROMM, P.O. 1980. A review of some physiological and toxicological responses of freshwater fish to acid stress. Environ. Biol. Fish. 5: 79–93.

HANCOCK, R. G. V. 1976. Low flux multielement instrumental neutron activation analysis in archaeometry. Anal. Chem. 48: 1443–1445.

HARVEY, H. H. 1980. Widespread and diverse changes in the biota of North American lakes and rivers coincident with acidification, p. 93–98. D. Drablos and A. Tollan [ed.] Proc. Int. Conf. Ecological Impact Acid Precipitation, Norway, 1980.

1981. Population responses of fishes in acidified water. Proc. Int. Conf. Acid Rain/Fish., Am. Fish. Soc. (In press)

HARVEY, H. H., AND C. LEE. 1980. Fishes of the La Cloche Mountain lakes of Ontario 1965–1980. MS Rep. Ontario Ministry of Natural Resources. 89 p.

HARVEY, H. H., R. C. PIERCE, P. J. DILLON, J. R. KRAMER, AND D. M. WHELPDALE. 1981. Acidification in the Canadian aquatic environment. NRCC No. 18475. National Research Council of Canada, Ottawa. 369 p.

HELWIG, J. T., AND K. A. COUNCIL [ed.] 1979. SAS User's Guide. 1979 Ed. SAS Institute Inc., Cary, North Carolina. 494 p.

HENRIKSEN, A., AND R. F. WRIGHT. 1978. Concentrations of heavy metals in small Norwegian lakes. Water Res. 12: 101–112.

HULTBERG, H. 1977a. Betydelsen av pH, humus - och saltinnehall i sjövatten för kvicksilverförekomst i gädda. Inst. Vatten Luftvårdsforskning. 9 p.

1977b. Thermally stratified acid waters in late winter — a key factor inducing self-accelerating processes which increase acidification. Water Air Soil Pollut. 7: 279–294.

IRVING, L., AND A. L. CHUTE. 1932. The participation of the carbonates of bone in the neutralization of ingested acid. J. Cell. Comp. Physiol. 2: 157–176.

JENSEN, K. W., AND E. SNEKVIK. 1972. Low pH levels wipe out salmon and trout populations in southernmost Norway. Ambio 1: 223–225.

JOHNSON, N. M. 1979. Acid rain: neutralization within the Hubbard Brook ecosystem and regional implications. Science (Washington, D.C.) 204: 497–499.

KIMURA, K., AND R. ICHIKAWA. 1976. Accumulation and retention of manganese-54 by marine goby. Radiat. Res. 17: 41. (Abstr.)

KOMADA, N. 1980. Growth of vertebral centra in the cypinid fish *Tribolodon hakonensis*. Jpn. J. Ichthyol. 26: 351–356.

KRUGER, P. 1971. Principles of activation analysis. Wiley-Interscience, New York. 522 p.

LEMANN, J. JR., E. J. LENNON, A. D. GOODMAN, J. R. LITZOW, AND A. S. RELMAN. 1965. The net balance of acid in subjects given large loads of acid or alkali. J. Clin. Invest. 44: 507–517.

LEMANN, J. JR., J. R. LITZOW, AND E. J. LENNON. 1966. The effects of chronic acid loads in normal man: further evidence for the participation of bone mineral in the defense against chronic metabolic acidosis. J. Clin. Invest. 45: 1608–1614.

LIKENS, G. E. 1976. Acid precipitation. Chem. Eng. News 54: 29–44.

LOCKHART, W. L., AND A. LUTZ. 1977. Preliminary biochemical observations of fishes inhabiting an acidified lake in Ontario, Canada. Water Air Soil Pollut. 7: 317–332.

MALLEY, D. F. 1980. Decreased survival and calcium uptake by the crayfish *Orconectes virilis* in low pH. Can. J. Fish. Aquat. Sci. 37: 364–372.

MCDONALD, D. G., H. HOBE, AND C. M. WOOD. 1980. The influence of calcium on the physiological responses of the rainbow trout, *Salmo gairdneri*, to low environmental pH. J. Exp. Biol. 88: 109–131.

MCDONALD, D. G., AND C. M. WOOD. 1981. Branchial and renal acid and ion fluxes in the rainbow trout, *Salmo gairdneri*, at low environmental pH. J. Exp. Biol. 93: 101–118.

MCWILLIAMS, P. G., AND W. T. W. POTTS. 1978. The effects of pH and calcium concentrations on gill potentials in the brown trout, *Salmo trutta*. J. Comp. Physiol. 126: 277–286.

MILLER, D. W., R. J. VETTER, AND G. J. ATCHINSON. 1980. Effect of temperature and dissolved oxygen on uptake and retention of ^{54}Mn in fish. Health Physics 38: 221–225.

MOUNT, D. I. 1973. Chronic effect of low pH on fathead minnow survival, growth and reproduction. Water Res. 7: 987–993.

MUNIZ, I. P., AND H. LEIVESTAD. 1980. Acidification — effects on freshwater fish, p. 84–92. D. Drablos and A. Tollan [ed.] Proc. Int. Conf. Ecological Impact Acid Precipitation, Norway, 1980.

NELSON, J. A. 1982. Physiological observations on developing rainbow trout, *Salmo gairdneri* (Richardson), exposed to low pH and varied calcium ion concentrations. J. Fish Biol. 20: 359–372.

NEUMAN, W. F., AND M. W. NEUMAN. 1958. The chemical dynamics of bone mineral. The University of Chicago Press, Chicago. 209 p.

NEVILLE, C. M. 1979. Influence of mild hypercapnia on the effects of environmental acidification on rainbow trout (*Salmo gairdneri*). J. Exp. Biol. 83: 345–349.

NOLAN, R. L. 1971. Fortran IV Computing and application. Addison-Wesley Publ. Co., Don Mills, Ontario. 365 p.

ODÉN, S., AND T. AHL. 1970. Försurningen av skandinaviska vatten. Särtryck ur Ymer, Årsbok. p. 103–122.

OGINO, C., AND G-Y. YANG. 1980. Requirements of carp *Cyprinus carpio* and rainbow trout *Salmo gairdneri* for dietary manganese and copper. Bull. Jpn. Soc. Sci. Fish. 46: 455–458.

OVERREIN, L. N., H. M. SEIP, AND A. TOLLAN. 1980. Acid precipitation — effects on forest and fish. SNSF-project Res. Rep. FR 19/80. 175 p.

PACKER, R. K., AND W. A. DUNSON. 1970. Effects of low environmental pH on blood pH and sodium balance in brook trout. J. Exp. Zool. 174: 65–71.

PENTREATH, R. J. 1976. Some further studies on the accumulation and retention of ^{65}Zn and ^{54}Mn by the plaice, *Pleuronectes platessa* L. J. Exp. Mar. Biol. Ecol. 21: 179–189.

PODOLIAK, H. A., AND H. K. HOLDEN. 1965. Distribution of dietary calcium to the skeleton and the skin of fingerling brown trout. New York Fish. Res. Bull. 33: 64–70.

RYAN, P. M., AND H. H. HARVEY. 1980. Growth responses of yellow perch *Perca flavescens* (Mitchill), to lake acidification in the La Cloche Mountain Lakes of Ontario. Environ. Biol. Fish. 5: 97–108.

ROSSELAND, B. O., I. SEVALDRUD, D. SVALASTOG, AND I. P. MUNIZ. 1980. Studies on freshwater fish populations — effects of acidification on reproduction, population structure, growth and food selection, p. 336–337. D. Drablos and A. Tollan [ed.] Proc. Int. Conf. Ecological Impact Acid Precipitation, Norway, 1980.

SCHEIDER, W. A., D. S. JEFFRIES, AND P. J. DILLON. 1979. Effects of acidic precipitation on Precambrian freshwaters in southern Ontario. J. Great Lakes Res. 5: 45–51.

SCHINDLER, D. W., R. H. HESSLEIN, R. WAGEMANN, AND W. S. BROECKER. 1980. Effects of acidification on mobilization of heavy metals and radionuclides from the sediments of a freshwater lake. Can. J. Fish. Aquat. Sci. 37: 373–377.

SCHOFIELD, C. L. 1976. Acid precipitation: effects on fish. Ambio 5: 228–230.

SCHOFIELD, C. L., AND J. R. TROJNAR. 1980. Aluminum toxicity to brook trout (*Salvelinus fontinalis*) in acidified water, p. 341–366. T. Y. Toribara, M. W. Miller, and P. E. Morrow [ed.] Proc. Conf. on Polluted Rain, Plenum Press, New York.

SEVALDRUD, I. H., AND I. P. MUNIZ. 1980. Sure vatn og innlandsfisket i Norge. Resultater fra intervjuundersøkelsene. 1974–1979. SNSF-project IR 77/80. 95 p.

SOMERS, K. M. 1980. Alterations of lake fish communities in response to acid precipitation and heavy metal loading near Wawa, Ontario. M.Sc. thesis, University of Toronto, Toronto, Ontario. 422 p.

SPRY, D. J., C. M. WOOD, AND P. V. HODSON. 1981. The effects of environmental acid on freshwater fish with particular reference to soft water lakes in Ontario and the modifying effects of heavy metals. A literature review. Can. Tech. Rep. Fish. Aquat. Sci. 999: 145 p.

SUNS, K., C. CURRY, AND D. RUSSELL. 1980. The effects of water quality and morphometric parameters on mercury uptake by yearling yellow perch. Ont. Min. Environ. Tech. Rep. LTS 80-1. 16 p.

UMEHARA, D., AND M. OGURI. 1978. Effects of environmental calcium content on plasma calcium levels in goldfish. Bull. Jpn. Soc. Sci. Fish. 44: 827–833.

WATER QUALITY CRITERIA. 1972. Superintendent of Documents, U.S. Government Printing Office, Washington, DC. 594 p.

WETZEL, R. G. 1975. Limnology. W. B. Saunders, Co., Toronto, Ontario. 743 p.

WHITE, A., P. HANDLER, E. L. SMITH, R. L. HILL, AND I. R. LEHMAN. 1978. Principles of biochemistry. McGraw-Hill Co., New York. 1492 p.

WOOD, J. M. 1980. The role of pH and oxidation–reduction potentials in the mobilization of heavy metals, p. 223–236. T. Y. Toribara, M. W. Miller, and P. E. Morrow [ed.] Proc. Conf. on Polluted Rain, Plenum Press, New York.

WRIGHT, R. F., T. DALE, A. HENRIKSEN, G. R. HENDREY, E. T. GJESSING, M. JOHANNESSEN, C. LYSHOLM, AND E. STOREN. 1977. Regional surveys of small Norwegian lakes. SNSF-project IR 33/77. 153 p.

WRIGHT, R. F., AND A. HENRIKSEN. 1978. Chemistry of small Norwegian lakes with special reference to acid precipitation. Limnol. Oceanogr. 23: 487–498.

Influence of Hook Size in the Hawaiian Deep-sea Handline Fishery

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RALSTON, S. 1982. Influence of hook size in the Hawaiian deep-sea handline fishery. Can. J. Fish. Aquat. Sci. 39: 1297 – 1302.

Experimental bottom fishing trials were conducted in the Northwestern Hawaiian Islands where four different hook sizes (Nos. 28, 30, 34, and 38) were fished simultaneously. Within this series the biggest hook is about 71% larger than the smallest hook. Alterations in gear within this range have no substantive effect on the catch of bottom fish. In all cases examined, variation in catch statistics associated with differing replications (days and sites) greatly exceeded any effect attributable to different hook sizes. It is concluded that for medium- and large-sized fish, the catch is reasonably representative of those fish which strike the hooks and that a sigmoid selection curve most accurately describes the selective properties of the gear in this fishery.

Key words: gear selection, hook size, bottom fish, replications

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Des pêches expérimentales sur le fond ont été pratiquées dans le nord-ouest des îles Hawaii avec quatre grandeurs d'hameçons différentes (n^{os} 28, 30, 34 et 38) utilisées simultanément. L'hameçon le plus gros de la série est environ 71 % plus gros que le plus petit. Entre ces extrêmes, des modifications à l'engin n'ont pas d'effet notable sur les prises de poissons de fond. Dans tous les cas étudiés, la variation des prises dans divers essais se répliquant (quant aux jours et aux sites) dépasse de beaucoup tout effet attribuable à différentes grandeurs d'hameçons. Nous concluons que, dans le cas de poissons de taille moyenne et grande, les prises sont assez représentatives des poissons qui mordent aux hameçons et qu'une courbe de sélection sigmoïde est celle qui décrit avec le plus de précision les propriétés sélectives de l'engin utilisé dans cette pêche.

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MUCH is known of the selective properties of both trawls and gill nets (e.g. ICNAF 1963), and Gulland (1969) describes briefly some methods for evaluating selection by these kinds of gear. In contrast, very little information concerning selection by hook-and-line fishing gear is available. The results of these few studies are somewhat contradictory, and currently it is difficult to generalize concerning the type and extent of bias likely to be present in samples obtained by this method of fishing.

A number of investigators have reported substantial bias in length–frequency samples derived from angling. For example, Fry (1949) found that hook-and-line fishing gear exhibited a dome-shaped selectivity curve for lake trout (*Salvelinus namaycush*), similar to that classically obtained from gill nets. Also, Fraser (1955) reported that smallmouth bass (*Micropterus dolomieui*) are increasingly susceptible to capture by hooks as fish size increases. Both of these authors concluded that size selection by hook and line is relatively severe and strongly dependent upon the size-classes sampled. Similarly, Brock (1962) found that length–frequency distributions of yellowfin tuna (*Thunnus albacares*) summarized from longline catches were quite different from those obtained from the purse-seine and live-bait fisheries. He found that small fish were poorly represented in the former fishery, whereas few large fish were sampled in the latter. Japanese researchers (Koike et al. 1968; Kanda et al. 1978; Koike and Kanda 1978) have suggested that samples of spiny goby (*Acanthogobius flavimanus*), mackerel (*Scomber japonicus*), and pond smelt (*Hypomesus olidus*) collected with hook and line demonstrate a bias towards an optimum catchable length which is in turn dependent upon hook size.

Other researchers have come to somewhat different conclusions. Chatwin (1958) reported that the hook-and-line selectivity curve of lingcod (*Ophiodon elongatus*) is sigmoidal and constant above a certain minimal size, analogous to selection curves obtained from trawl fisheries (Gulland 1969). Both McCracken (1963) and Saetersdal (1963) reported similar findings while studying Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). In addition, these authors found that variation in hook size tended to shift the

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minimum size of capture but did not affect the catch of large fish. Moreover, Allen (1963) concluded that samples of New Zealand trout obtained by fly-fishing were unbiased. Similarly, Leclerc and Power (1980) found fly-fishing to be the least selective of three different methods of sampling for brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*).

This study began as an attempt to evaluate the type and extent of size bias present in the catch of bottom fish landed in the Hawaiian deep-sea handline fishery (Hawaii Department of Land and Natural Resources 1979; Ralston 1981; Ralston and Polovina 1982). Because of the conflicting nature of previous work on this topic, it became necessary to investigate the process of gear selection in this particular fishery. A selection curve can be calculated by comparing independent, unbiased samples with hook-and-line catch statistics. At present there are no similar data concerning stocks of bottom fish in Hawaii and it is not possible to calculate selection curves for this fishery. However, by examining the effect of hook size variation on the catch of bottom fish, one can infer much about the selective properties of fishing hooks.

Methods

Fishing trials were conducted during four research cruises to the Northwestern Hawaiian Islands on the 23-m, 109 gross ton R/V *Easy Rider*. This vessel is capable of multiple fishing activities and is typical of the larger, more powerful craft which have recently entered the offshore handline fishery in Hawaii.

The boat was equipped with three deep-sea bottom fishing rigs composed of Charlin hydraulic motors, Pacific King fishing reels, and ~ 400 m of 150-kg test, braided prestretched Dacron line. Standard equipment on each rig included four #34 Tankichi ulua hooks attached to 75-kg test monofilament leaders and a 2-kg welded reinforcement-bar weight.

The effect of variation in hook size on the catch of bottom fish was studied by simultaneous fishing with hooks of different sizes (Fig. 1). Each of the three fishing reels was rigged with one each of the four differently sized hooks (Nos. 28, 30, 34, and 38) to control for line and fisherman effects. To control for a possible position effect, the locations of the four hooks on each line were determined at random. During experimental trials each fishing line was monitored individually. All hooks were baited with equivalent pieces of cut frozen squid and released to the bottom. The fate of each hook was recorded upon retrieval to the surface. When fish were landed the species and the fork length (FL) or total length (TL) in centimetres were noted, as were loss of bait and broken hooks when appropriate.

Data were summarized according to each day of fishing trials ($n = 17$), which individually were treated as experimental replications. Fishing took place at Necker Island, French Frigate Shoals, Maro Reef, and Midway and Kure Atolls during March and October 1979, and November 1980. Catch statistics included the number and size composition of each species landed on the four different sizes of hooks. These data were analyzed as randomized complete blocks in parametric two-way analyses of variance (ANOVA) when samples were sufficiently abundant, although for two species the size composition data were sparse. In these situations the data were pooled across replications and a simple one-way parametric ANOVA was performed (hook size as treatment effect). Similarly, for the same two species the Friedman test, a nonparametric two-way analysis (Tate and Clelland 1957; Conover 1980), was applied to the number of individuals landed per day because the data matrix contained many zeros.

Results

A total of 1110 fish were landed and measured during the four research cruises. The catch was composed mainly of opakapaka (*Pristipomoides filamentosus*), which alone accounted for 50% of the total. This snapper (Lutjanidae), the target species, is usually found in waters 100–200 m deep. Lesser numbers of other species were also taken: the hapuupuu (*Epinephelus quernus*), a grouper (Serranidae), and the pig ulua (*Pseudocaranx dentex*), a jack (Carangidae). These two species comprised 17 and 21%, respectively, of the catch. Analyses of gear selection in each of these three species were conducted independently.

Number of Opakapaka

Adequate samples of opakapaka were taken on 12 of the 17 possible trial days. The data were square-root transformed ($\sqrt{x}$) because some cell entries were small whole numbers leading to heterogeneous variances. Application of Tukey's test showed no evidence of non-additivity after transformation ($P \simeq 0.20$, Snedecor and Cochran 1967). The ANOVA showed that the four different sizes of hooks did not catch significantly different numbers of opakapaka per day, although the F statistic was only marginally insignificant ($0.10 > P > 0.05$). Based upon examination of the treatment means there was the suggestion that hook size may affect the number of opakapaka caught in a day, the three smaller hooks being more effective. The data were subsequently analyzed as a one-way χ^2 test under the null hypothesis that the total number of opakapaka caught on each of the four different hook sizes, pooled across all replications, should be equal. This analysis is appropriate because all hooks were always fished simultaneously and the experiment was therefore completely randomized, with catch per hook following the multinomial distribution. Furthermore, a two-way χ^2 analysis of the data showed no interaction between replications and hooks in their joint effect on catch per day ($P \simeq 0.80$). The one-way calculation yielded a significant value ($P \simeq 0.03$), however, demonstrating that smaller hooks are more effective than size No. 38 hooks in catching opakapaka.

A highly significant replication effect is evident in these data (ANOVA, $P << 0.005$), implying that the number of opakapaka caught among differing days and sites is highly variable. The total catch, pooled across hooks, ranged from a high of 58 to a low of 3 individual opakapaka landed per day.

Size of Opakapaka

The effect of hook size variation on the size (FL, cm) of

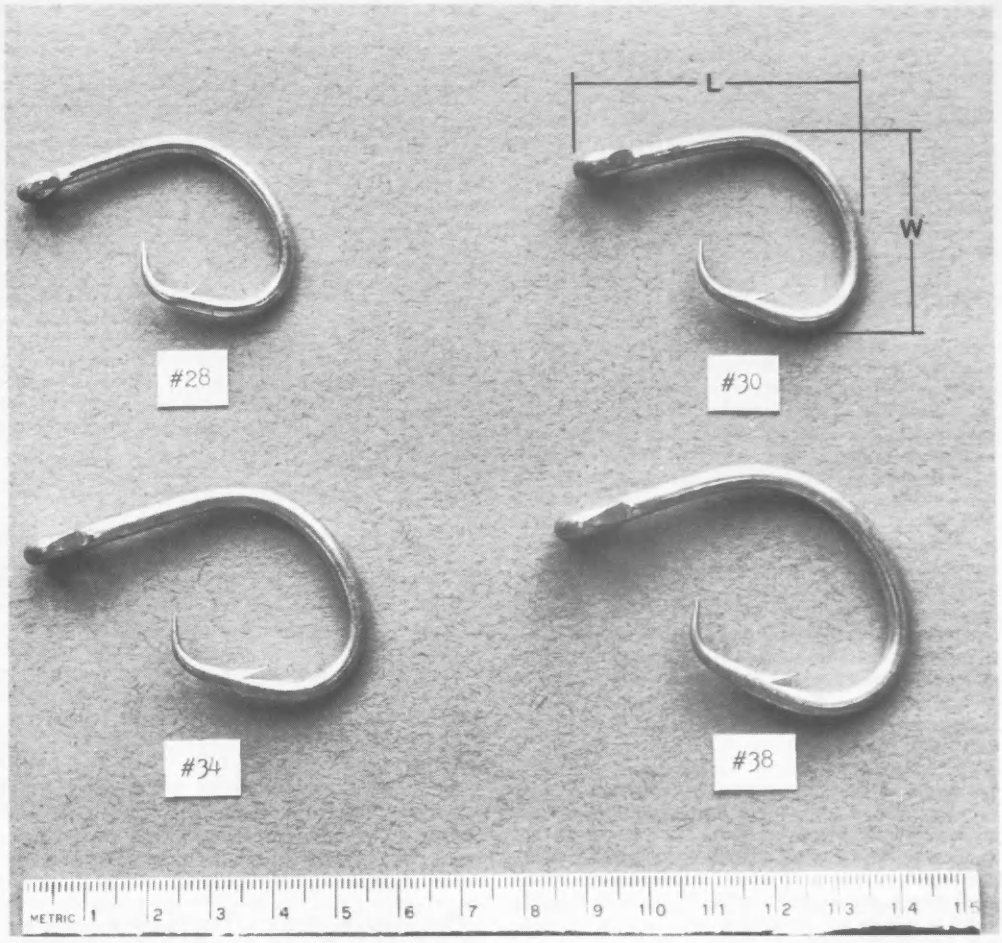

FIG. 1. Four sizes of Tankichi ulua hooks used in experimental fishing trials. The absolute size of a hook was calculated as the product of its length (L) and width (W).

opakapaka landed was examined by means of a two-way ANOVA with repeated observations of unequal sample size (Dixon 1977, program BMDP2V). The analysis was treated as a mixed model with hooks as fixed effects and days as random effects.

Over the size range of hooks tested (Nos. 28–38) there is no indication of a treatment effect. Large hooks appear to be as successful as small ones in catching small fish and vice versa (ANOVA, $P \simeq 0.25$). In comparison, the day of fishing (replication) very strongly affected the size of opakapaka landed ($P << 0.005$). The mean size of opakapaka caught among different days ranged from 37 to 61 cm FL. Most of this variation can be attributed to differences between French Frigate Shoals and Maro Reef in the average size of fish they yield. Furthermore, the analysis suggests that there is no interaction between hook and day effects.

NUMBER OF HAPUUPUU

Sufficient numbers of hapuupuu for analysis were landed on 15 of the 17 possible experimental fishing days. Variable hook size had no discernible effect on the number of hapuupuu landed (Friedman test, $P >> 0.05$) whereas the day fished had a profound effect on this statistic ($P << 0.01$). This is evidenced by the fact that the numbers of hapuupuu caught on the different hooks, pooled across days, ranged from 24 to 35 whereas the numbers caught on different days ranged from 1 to 24. A χ^2 test examining the total numbers of

hapuupuu landed, pooled across all replications, was insignificant ($P \simeq 0.55$).

Size of Hapuupuu

Variation in hook size had no detectable effect on the size of hapuupuu landed, although the F statistic was but marginally insignificant (one-way ANOVA, $P \simeq 0.10$). Because variation attributable to different days of fishing could not be factored out, a more thorough sampling program might demonstrate significant hook effects (larger hooks tending to catch, on average, larger fish).

Number of Pig Ulua

Sufficient numbers of pig ulua for analysis were taken on 10 of the 17 experimental fishing days. Hook size did not significantly affect the number of pig ulua caught (Friedman test, $0.10 > P > 0.05$). The borderline condition of the test statistic could well be due to sampling error (type I) because no trend was evident in the success of the various hook sizes in capturing this species. Hooks of intermediate size (Nos. 30 and 34) seemed to perform slightly better than the extremes (Nos. 28 and 38). Furthermore, a χ^2 test of the treatment totals, pooled across all replications, showed no difference due to hooks ($P \simeq 0.18$). In contrast, the day of fishing (replications) exerted a strong effect on the numbers landed (Friedman test, $P << 0.01$). The numbers of pig ulua landed on different days ranged from 1 to 47. As with the opakapaka, differences in catch rates of pig ulua between the study sites at French Frigate Shoals and Maro Reef probably account for the preponderance of this effect.

Size of Pig Ulua

All pig ulua data were simply classified according to the size of hook the sample was landed with because the numbers caught were limited. Variation in hook size (Nos. 28–38) had no effect on the size of pig ulua landed (one-way ANOVA, $P >> 0.05$). The mean sizes of fish caught, in ascending order of hook size, were 65.3, 65.1, 65.7, and 65.4 cm FL.

Total Numbers of Fish

To assess whether variation in hook size affects total catch of bottom fish I included the three species already treated, and the incidental catch of kahala (*Seriola dumerili*), ehu (*Etelis carbunculus*), gindai (*Pristipomoides zonatus*), and other species. Catch rate was measured on a daily basis as the mean number of fish caught per drift of the vessel. Drifts generally ranged between 10 and 40 min duration. The computations include all 17 of the experimental fishing days and the analysis performed was a two-way ANOVA.

Variable hook size had no detectable effect on the mean number of fish caught per drift ($P >> 0.10$). In ascending order of hook size, the treatment means for hooks were 0.99, 0.97, 0.92, and 0.86 individuals per hook per drift. Similarly, when the total catch of all species is pooled across all replications, a χ^2 test of the treatment totals is insignificant ($P \simeq 0.22$). In contrast, the day fished (replication) exhibited a strong effect on total catch rate ($P << 0.005$), with replication means ranging from 0.15 to 2.35 individuals per hook per drift. These results indicate that variation in hook size from No. 28 to No. 38 has no appreciable effect on bottom fish catch rate.

TABLE 1. Summary of all analyses performed in assessment of gear selection. Probabilities (P) refer to the chance of obtaining a test statistic under the null hypothesis of no difference due to treatment or replication. N.S. = not significant.

Variable examined	Treatment (hooks)	Replication (d)
Number of opakapaka	$P < 0.05$	$P << 0.005$
Size of opakapaka	N.S.	$P << 0.005$
Number of hapuupuu	N.S.	$P << 0.005$
Size of hapuupuu	$P \simeq 0.10$	—
Number of pig ulua	$0.10 > P > 0.05$	$P << 0.005$
Size of pig ulua	N.S.	—
Total numbers of fish	N.S.	$P << 0.005$
Bait loss	N.S.	$P << 0.005$

Bait Loss

The effectiveness of different sizes of hooks at retaining bait provides another means of ascertaining selection. If one hook size loses bait more often than another, it might be concluded that the two hooks draw different samples from the population, assuming strike rate is unaffected by hook size.

Eleven of the 17 possible trial days were used in this analysis, which shows that variation in hook size had no appreciable effect on the mean number of baits lost per drift whereas the day fished had a highly significant effect on this quantity (two-way ANOVA, $P \simeq 0.20$ and $P < 0.005$, respectively). The mean numbers of baits lost per hook per drift among the four hooks, in ascending order of hook size, were 1.65, 1.50, 1.43, and 1.42 whereas among the days fished these figures ranged from 0.82 to 2.11.

Discussion

This simple attempt at analyzing the nature of gear selection in the Hawaiian deep-sea handline fishery demonstrates two basic points. In all six situations examined, the day fished had a highly significant effect on the variables measured, whereas in only one case out of eight was a significant effect due to hook size demonstrated (Table 1). It is important to realize that the range of hook sizes used here is fairly typical of those in the fishery although hooks smaller than this series are occasionally employed.

Based on these facts it is reasonable to conclude that alterations in gear within this range of sizes have very little effect on the outcome of bottom fishing in Hawaii. It is readily apparent that variation in both catch rates and species size composition within this fishery are caused predominantly by differences between fishing banks, months, and days (replications). This variation is more than enough to mask any real hook effects at the present level of sampling, although in one situation (number of opakapaka) a significant effect due to hooks was revealed.

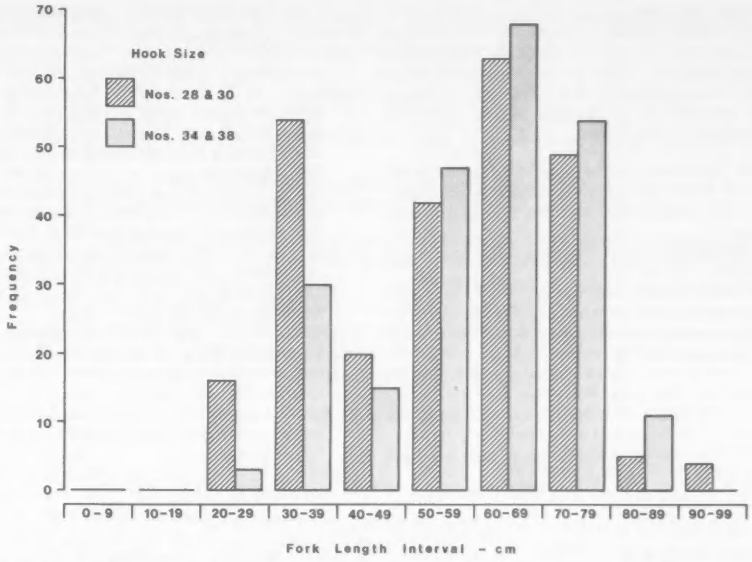

FIG. 2. Combined length–frequency distributions of opakapaka, hapuupuu, and pig ulua which are pooled according to capture on small hooks (Nos. 28 and 30) or large hooks (Nos. 34 and 38).

That the hook-and-line fishery is relatively insensitive to moderate changes in gear is contrary to expectation if the selection curve for hooks were dome shaped. Thus, it is reasonable to presume that in this fishery, selection by hooks is better described by a trawl type or sigmoidal selection curve, with little differential sampling of the larger individuals in the population (e.g. Chatwin 1958; McCracken 1963; Saetersdal 1963). This presumption is supported by the data presented in Fig. 2. Here the combined catches of opakapaka, hapuupuu, and pig ulua have been pooled into two groups: those fish caught on large hooks (Nos. 34 and 38) and those caught on small hooks (Nos. 28 and 30). The histograms suggest that for medium- and large-sized fish (≥45 cm FL) the large and small hooks draw more or less equivalent samples. However, the small hooks appear to have been more effective in capturing small fish (<45 cm FL). These results are compatible with the hypothesis that the selection curve for hooks is sigmoidal. For these reasons it is reasonable to conclude that the catch of bottom fish ≥45 cm FL is likely to be representative of the population sampled.

If a sigmoidal selection curve is postulated for this hook-and-line gear, there should exist a minimum size of capture. That the mean size landed for each species, when treated individually, was insensitive to changes in hook size (Table 1) is contrary to the findings of both McCracken (1963) and Saetersdal (1963). This discrepancy could be due to constraints imposed on the sampling process by the behavior of the fish (see for example Allen 1963). A more likely explanation is insufficient sampling.

Furthermore, the range of hook sizes which were utilized in these experiments (Fig. 1) was not broad. If hooks spanning a greater size range had been employed, it is more likely that a treatment effect on mean size of capture would have been conclusively demonstrated for each species. For example, it is possible to compute an index which measures the size range of hooks used by forming the ratio of the absolute sizes of the largest hook used to the smallest. Hook size is calculated as the product of the length and width of a hook (Fig. 1). In this study the largest hook used (No. 38) was 71% greater in size than the smallest hook (No. 28). In contrast, Koike et al. (1968) and Kanda et al. (1978) used series of hooks in which the largest sizes were 215 and 111%, respectively, larger than the smallest of sizes. Both studies reported shifts in the size composition of the catch depending upon the size of hooks used. Clearly, if hook sizes are highly dissimilar the size composition of the catch must ultimately vary. In spite of this, the hook sizes I used are typically those in use by the fishermen. Moreover, Saetersdal (1963) reported a change in the selective characteristics of fishing hooks which differed in size by only 76%. Consequently, it may be concluded that within the context of the Hawaiian deep-sea handline fishery, little size bias attributable to hook-and-line gear manifests itself in the catch of bottom fish.

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ALLEN, K. R. 1963. The influence of behaviour on the capture of fish with baits, p. 5–7. *In* The selectivity of fishing gear. Spec. Publ. No. 5. Int. Comm. Northwest Atl. Fish., Dartmouth, N.S., Canada.

BROCK, V. E. 1962. On the nature of the selective fishing action of longline gear. Pac. Sci. 16: 3–14.

CHATWIN, B. M. 1958. Mortality rates and estimates of theoretical yield in relation to minimum commercial size of lingcod (*Ophiodon elongatus*) from the Strait of Georgia, British Columbia. J. Fish. Res. Board Can. 15: 831–849.

CONOVER, W. J. 1980. Practical nonparametric statistics. 2nd ed. John Wiley & Sons, New York, NY. 493 p.

DIXON, W. J. [ed.] 1977. BMDP-77 biomedical computer programs, P-series. Univ. California Press, Los Angeles, CA. 880 p.

FRASER, J. M. 1955. The smallmouth bass fishery of South Bay, Lake Huron. J. Fish. Res. Board Can. 12: 147–177.

FRY, F. E. J. 1949. Statistics of a lake trout fishery. Biometrics 5: 27–67.

GULLAND, J. A. 1969. Manual of methods for fish stock assessment. Part. I. Fish population analysis. FAO Man. Fish. Sci. 4. 154 p.

HAWAII DEPARTMENT OF LAND AND NATURAL RESOURCES. 1979. Hawaii fisheries development plan. Department of Land and Natural Resources, State of Hawaii. 297 p.

ICNAF. 1963. The selectivity of fishing gear. Spec. Publ. No. 5. Int. Comm. Northwest Atl. Fish., Dartmouth, N.S., Canada. 225 p.

KANDA, K., A. KOIKE, S. TAKEUCHI, AND M. OGURA. 1978. Selectivity of the hook for mackerel, *Scomber japonicus* Houttuyn, pole fishing. J. Tokyo Univ. Fish. 64: 109–114.

KOIKE, A., AND K. KANDA. 1978. Selectivity of the hook of pond smelt, *Hypomesus olidus*. J. Tokyo Univ. Fish. 64: 115–123.

KOIKE, A., S. TAKEUCHI, M. OGURA, K. KANDA, AND C. ARIHARA. 1968. Selection curve of the hook of long line. J. Tokyo Univ. Fish. 55: 77–82.

LECLERC, J., AND G. POWER. 1980. Selectivity of fly-fishing, spinning and gillnet for brook charr and ouananiche in a large northern Quebec river. Environ. Biol. Fish. 5: 181–184.

MCCRACKEN, F. D. 1963. Selection by codend meshes and hooks on cod, haddock, flatfish, and redfish, p. 131–155. *In* The selectivity of fishing gear. Spec. Publ. No. 5. Int. Comm. Northwest Atl. Fish., Dartmouth, N.S., Canada.

RALSTON, S. 1981. A study of the Hawaiian deepsea handline fishery with special reference to the population dynamics of opakapaka, *Pristipomoides filamentosus* (Pisces: Lutjanidae). Ph.D. dissertation, Univ. Washington, Seattle, WA. 205 p.

RALSTON, S., AND J. J. POLOVINA. 1982. A multispecies analysis of the commercial deep-sea handline fishery in Hawaii. Fish. Bull. U.S. 80. (In press)

SAETERSDAL, G. 1963. Selectivity of long lines, p. 189–192. *In* The selectivity of fishing gear. Spec. Publ. No. 5. Int. Comm. Northwest Atl. Fish., Dartmouth, N.S., Canada.

SNEDECOR, G. W., AND W. G. COCHRAN. 1967. Statistical methods. Iowa State Univ. Press, Ames, IA. 593 p.

TATE, N. W., AND R. C. CLELLAND. 1957. Nonparametric and shortcut statistics in the social, biological, and medical sciences. Interstate Printers and Publ., Inc., Danville, IL. 171 p.

Population Characteristics of Juvenile Coho Salmon (*Oncorhynchus kisutch*) Overwintering in Riverine Ponds[1]

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PETERSON, N. P. 1982. Population characteristics of juvenile coho salmon (*Oncorhynchus kisutch*) overwintering in riverine ponds. Can. J. Fish. Aquat. Sci. 39: 1303 – 1307.

Survival and growth from immigration to smolt outmigration differed substantially between pond populations of juvenile coho salmon (*Oncorhynchus kisutch*). In Pond 1 (the deeper, less-productive pond) overall survival was 78% but average fish weight increased only 49%, whereas in Pond 2 (the shallow, more-productive pond) survival was only 28% but average fish weight increased 94%. Diet of resident coho in the early spring was characterized by chironomid larvae and newly emerged adults in Ponds 1 and 2, respectively. Manipulation of pond morphometry may have potential for enhancing coho stocks.

Key words: coho, pond, winter habitat, survival, growth, diet

PETERSON, N. P. 1982. Population characteristics of juvenile coho salmon (*Oncorhynchus kisutch*) overwintering in riverine ponds. Can. J. Fish. Aquat. Sci. 39: 1303 – 1307.

La survie et la croissance entre l'immigration et l'émigration comme smolts diffèrent de façon substantielle entre populations d'étangs de jeunes saumons coho (*Oncorhynchus kisutch*). Dans l'étang 1, plus profond et moins productif, la survie générale est de 78 %, mais le poids moyen des poissons n'augmente que de 49 %. Par contre, dans l'étang 2, moins profond et plus productif, la survie n'est que de 28 %, mais le poids moyen des poissons augmente de 94 %. Le régime des saumons résidents au début du printemps est caractérisé par des larves de chironomides et d'adultes nouvellement émergés dans les étangs 1 et 2 respectivement. Il se peut que la modification de la morphométrie d'un étang offre des possibilités de mise en valeur des stocks de saumons coho.

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JUVENILE coho salmon (*Oncorhynchus kisutch*) seasonally seek out winter refuge areas throughout their range in North America. Small tributary streams (Bustard and Narver 1975) and riverine ponds (Peterson 1982) are especially preferred winter habitat. However, the ecology of juvenile salmonids in such ponds is not well documented. The purpose of this study was to compare the survival, growth, and diet of juvenile coho populations overwintering in two natural riverine ponds.

Study Area

The study ponds lie in old flood plains of the Clearwater River (Peterson 1982), originating as cutoff river meanders. Coincidentally, these sites receive near-surface groundwater flow overland from nearby terraces, and function as flow-through systems connected to the river by small outlet streams. Pond 1 is the deeper of the two ponds, and whereas Pond 2 is half again as large, it is shallow over most of its area (Table 1).

Species of fish other than coho that commonly utilize the ponds are cutthroat trout (*Salmo clarki*), prickly sculpin (*Cottus asper*), and western speckled dace (*Rhinichthys osculus*). Less frequently observed species are steelhead trout (*S. gairdneri*) and torrent sculpin (*C. rotheus*). Avian predators such as kingfishers, herons, and mergansers are commonly observed on the ponds. River otters have also been seen on both ponds, but less frequently.

Shoreline vegetation consists mainly of red alder (*Alnus rubra*), big leaf maple (*Acer macrophyllum*), Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), salmonberry (*Rubus spectabilis*), blackberries (*R. laciniatus*), sword fern (*Polystichum* sp.), sedges (*Carex* sp.), and horsetail (*Equisetum* sp.). Yellow pond lilies (*Nuphar variegatum*) grow in areas less than 1.0 m deep. Other common aquatic macrophytes include at least two species of *Potamogeton* and one bladderwort (*Utricularia* sp.). *Potamogeton* encroaches to depths of about 1.5 m, but deeper areas lack rooted plants.

Methods and Materials

Fish traps were located on the pond outlet streams that

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caught all fish migrating in either direction. All immigrant coho caught during the first and last weeks of November were marked differently with a cold brand. During these periods these same fish were also separated into two groups — those >80 mm and those <80 mm, and marked differently. This artificial separation caused the length distribution of the group of smaller fish to be skewed to the right. The group of larger fish was affected in the opposite direction, but to a lesser degree as 80 mm was considerably less than the mean of the normally distributed combined population. In addition, one group was marked in each pond after being captured by electroshocking in February, without respect to size of fish. Another such group was marked in March in Pond 2. Marked groups were designated by four-letter codes (Peterson 1982). Twenty and 15% of the population were marked in the fall in Ponds 1 and 2, respectively. Growth and survival of marked fish were assumed to be representative of the entire population. A comparison made the following spring of the lengths of marked and unmarked fish revealed no statistical difference.

Because traps were inoperable for short periods during some winter storms, an estimate of the total fall immigration was made by expanding the number of fish marked in the fall by the proportion of marked to unmarked smolts. This assumes that (1) all smolts were caught, (2) all marked smolts were identified, (3) the only recruitment to the smolt population was from fall immigrants, and (4) marking did not increase overwinter mortality of marked fish.

Assumption three is invalid as scale analysis of large fish showed some were 2 yr old and probably did not originate from the fall population. To identify the number of these smolts, the minimum length of 2-yr-old smolts from each pond was determined. The proportion of smolts greater than this size was then determined for all groups combined that were marked in the fall. This proportion was applied to the total number of outmigrants to estimate the number of smolts in the 2-yr-old size range that probably originated as fall immigrants. These fish were then subtracted from the total number of smolts in the 2-yr-old size range. The remaining large fish were assumed to be 2-yr-old smolts from the previous winter, and subtracted from the total prior to calculation of the marked-to-unmarked smolt proportion. In addition, adjustments were made in Pond 1 for a 50% contribution of the 450 fry that immigrated the previous spring. No such adjustment was made in the Pond 2 data as a blockage in the stream probably prevented fry from reaching the pond.

Growth statistics for the marked groups were determined by first calculating an average length for the group. Then correlative weights for these lengths were calculated from length–weight regressions that were developed for spring and fall populations for each pond. These weights were used to illustrate growth differences between ponds. Statistically, the difference in smolt size was measured by testing the difference in average lengths of marked groups with an unpaired *t*-test (Snedecor and Cochran 1967).

DIET

Stomach contents from 15 and 30 fish from Ponds 1 and 2, respectively, were collected by electroshocking in early afternoon on consecutive days in February. Contents of the foregut were flushed as described by Meehan and Miller (1978). Prey items from each sample were sorted, usually to family. All items from each taxon were placed on a predried and weighed filter. Unidentifiable material left after sorting was filtered onto another filter. All filters and contents were then dried at 60°C for 24 h and reweighed to the nearest 0.1 mg. Prey data were processed through a diet analysis program (Swanson and Simenstad 1978). Dry weight of stomach contents, expressed as a percent of the dry weight of the fish, which was assumed to be 0.20 wet weight, were compared between ponds with a nonparametric rank test.

TABLE 1. Physical characteristics of the study ponds.

Characteristic	Pond 1	Pond 2
Area, ha	0.85	1.29
Volume, m^3	10 300	7600
Maximum depth, m	3.5	1.3
Percent area <0.75 m deep	47	84
Percent area >1.2 m deep	38	0.3

TABLE 2. Numbers of immigrant juvenile coho in the fall and emigrant smolts for Ponds 1 and 2.

Pond	No. of fall immigrants		No. of spring smolts
	Trapped	Total estimate	
Pond 1	3297	4100	3613[a]
Pond 2	4029	5430	1534[a]
Total	7326	9530	5147[a]

[a]Includes smolts recruited from holdover and fry populations, 414 and 14 for Ponds 1 and 2, respectively.

BENTHOS

Benthos samples collected in December, February, and April were stratified by three stations selected for depth and similarity of substrate character. Three replicate samples were taken at each station on all dates. Samples were removed with a 10-cm-diameter core sampler which removed an undisturbed sample from the flocculent organic sediments of the ponds. Cores were washed through a 420-μm sieve and preserved in 70% ethanol. Animals were separated from the detritus and identified to family. Station samples were counted and placed on predried and weighed filters for drying at 60°C for 24 h and reweighed to the nearest 0.1 mg.

Benthos count and weight data were analyzed for independence of variance and distribution character (Elliott 1977). Tests indicated count data should be transformed to logarithms, but weight data were suitable for parametric testing.

Analysis of variance was used to test differences in sample dry weights and transformed ($\log_{10}$) count data between ponds. Within ponds, analysis of variance was used to test for differerences due to the effects of month and station.

PHYSICAL MEASUREMENTS

Pond temperatures at a 0.3-m depth were recorded con-

TABLE 3. Absolute survival and instantaneous mortality rates of juvenile coho in specific marked groups for Ponds 1 and 2.

Mark	Pond	Median date in	Median date out	Median residence (d)	Number in	Number out	Percent survival	Instantaneous mortality (Z)
RMNV	Pond 1	Nov. 7, 1977	April 25, 1978	169	578	464	80.3	0.001
	Pond 2	Nov. 10, 1977	March 21, 1978	131	408	127	31.1	0.009
RMSV	Pond 1	Nov. 8, 1977	May 12, 1978	185	39	29	74.4	0.002
	Pond 2	Nov. 10, 1977	March 30, 1978	140	26	7	26.9	0.009
RMNT	Pond 1	Nov. 29, 1977	May 3, 1978	155	49	25	51.0	0.004
	Pond 2	Nov. 29, 1977	March 26, 1978	117	101	11	10.9	0.019
RMST	Pond 1	Nov. 30, 1977	May 12, 1968	163	12	8	66.7	
	Pond 2	Nov. 29, 1977	March 30, 1978	121	11	1	9.1	
RPEV[a]	Pond 1	Feb. 25, 1978	May 4, 1978	68	64	51	79.7	0.003
	Pond 2	Feb. 26, 1978	March 26, 1978	28	112	55	49.1	0.025

[a]Captured by electroshocking and marked while in pond residence.

tinuously on chart thermographs. Water samples taken at three stations at several depths for dissolved oxygen determinations were analyzed chemically.

Results

Outmigration of Smolt Populations

Three thousand, six hundred and thirteen coho smolts emigrated from Pond 1, 3200 of which originated as fall immigrants, whereas Pond 2 yielded only 1534 smolts of which 1520 were fall immigrants (Table 2). In Pond 2 the peak in migration occurred in late March, but in Pond 1 it occurred in late April and remained high until the middle of May. Larger fish migrated first from both ponds and the earlier migration observed in Pond 2 was the outcome of more rapid growth there.

Survival of Pond Populations

Overall survival of pond residents was 78 and 28% in Ponds 1 and 2, respectively. Regardless of fish size or time of pond entry juvenile coho in Pond 1 showed consistently higher survival than those in Pond 2 (Table 3). Because residence time was appreciably different between ponds, instantaneous mortality rates were compared, and they substantiated the considerably higher mortality in Pond 2.

Smaller fish in both ponds (RMSV and RMST groups) showed slightly poorer survival in both absolute and instantaneous terms. Fish which entered the ponds in late November after most of the fall population had already immigrated incurred higher mortality than did those which entered in the 1st week in November. Small sample sizes of small fish entering both ponds in late November disallowed further comparison of instantaneous mortality rates.

Based on population estimates derived by expanding the smolt populations by spring mortality, as determined by marking (RPEV groups), survival decreased in time in both ponds. Prior to late February little mortality had occurred in Pond 1, whereas nearly 50% of the population had died in Pond 2 (Fig. 1).

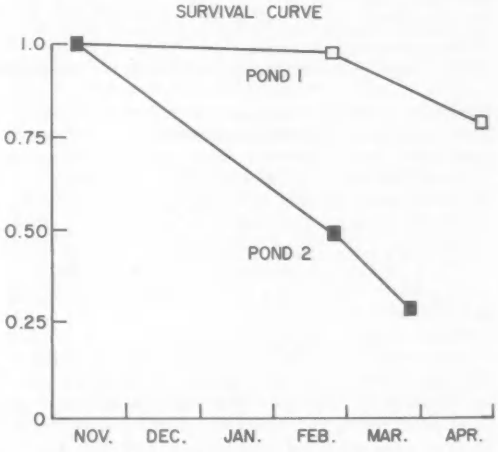

FIG. 1. Survival of pond populations through time.

Growth of Pond Residents

The average size of smolts in all groups in Pond 2 was significantly larger ($P < 0.01$) than that of the matching group in Pond 1 (Table 4). These apparent growth differences occurred in spite of an appreciably shorter median residence time in Pond 2.

Between fall entry and late February, average growth of fish in Pond 1 was nil. During this same period, apparent growth in Pond 2 was significant, with an average weight increase of 83%.

Smaller immigrants (RMSV groups) had caught up in size with their larger cohorts (RMNV-marked fish) by spring outmigration. However, the smaller immigrants remained in the pond an average of 16 and 9 d longer in Ponds 1 and 2, respectively, than did their cohorts in the larger size category at pond entry.

Diet

The Chironomidae were the most important prey for fish in

TABLE 4. Absolute and relative weight increases of juvenile coho overwintering in study ponds.

Mark	Pond	Median date marked	Median date recaptured	Median residence in days	Number in	Number out	Mean size in grams	Mean size out grams	Average increase	
									Absolute grams	Relative percent
RMNV	Pond 1	Nov. 7, 1977	April 25, 1978	169	578	464	8.77	13.09	4.32	49.3
	Pond 2	Nov. 10, 1977	March 21, 1978	131	408	127	9.34	18.14	8.80	94.2
RMNV	Pond 1	Nov. 7, 1977	Feb. 25, 1978	110	578	8[a]	8.77	8.54	−0.23	−2.6
	Pond 2	Nov. 10, 1977	Feb. 26, 1978	108	408	13[a]	9.34	17.05	7.71	82.5
RMSV	Pond 1	Nov. 8, 1977	May 12, 1978	185	39	29	4.59	12.17	7.58	165.1
	Pond 2	Nov. 10, 1977	March 30, 1978	140	26	7	5.11	19.31	14.20	277.9
RMNT	Pond 1	Nov. 29, 1977	May 3, 1978	155	49	25	7.87	12.33	4.46	56.7
	Pond 2	Nov. 29, 1977	March 26, 1978	117	101	11	8.72	16.40	7.68	88.1
RMST	Pond 1	Nov. 30, 1977	May 12, 1978	163	12	8	5.04	13.50	8.46	167.9
	Pond 2	Nov. 29, 1977	March 30, 1978	121	11	1	4.97	17.60	12.63	254.1
RPEV[b]	Pond 1	Feb. 25, 1978	May 4, 1978	68	64	51	9.49	13.89	4.40	46.4
	Pond 2	Feb. 26, 1978	March 26, 1978	28	112	55	16.89	19.95	3.06	18.1

[a]Recaptured by electroshocking.
[b]Captured by electroshocking and marked while in pond residence.

both ponds, occurring in all stomachs. In Pond 1, chironomid larvae comprised 72% of the diet numerically, and 40% gravimetrically (Table 5). In Pond 2, adult chironomids were more important than were the larvae. Qualitative observations of insect emergence indicated there was a protracted emergence of chironomids in Pond 2 during late winter and early spring, and that coho fed heavily on this emergence. Adults occurred in 87% of the stomachs and accounted for 56% of the Pond 2 diet gravemetrically (Table 6). Limnephilid caddis fly larvae and baetid mayfly nymphs were next in order of importance in Ponds 1 and 2, respectively.

Tested with a nonparametric rank test, total dry weight of stomach contents (expressed as a percentage of the calculated dry weight of the fish) showed no statistical difference between ponds. However, when plant and unidentifiable weight fractions were subtracted from all data, fish from Pond 2 (scant plant material in their guts) had higher dry weights ($P < 0.05$). Pond 1 fish ingested a higher proportion of plant material apparently incidentally with encased chironomid and limnephilid larvae.

BENTHOS

Taxonomic composition of the benthos from both ponds was typical of other pond environments. Diptera larvae, principally Chironomidae, predominated.

An analysis of variance on sample dry weights that tested the effects of pond, month, and station showed the only significant main effect was due to pond ($P < 0.01$). A duplicate analysis of transformed ($\log_{10}$) count data indicated a similar effect ($P < 0.01$).

Sample dry weights compared by station between ponds showed that all stations in Pond 2 had greater mean dry weights than those in Pond 1; however, only station one was statistically different ($P < 0.05$) (Fig. 2). This station is the most important to compare between ponds because it represents habitat typical of ~ 50 and 80% of Ponds 1 and 2, respectively.

TABLE 5. Frequency of occurrence, numerical and gravimetric composition of major invertebrate taxa in the diet of juvenile coho in Pond 1.

Prey taxa	Frequency of occurrence	Composition	
		Numerical	Gravimetric
Chironomidae	100.00	71.9	39.6
Chironomidae[a]	60.00	4.1	7.6
Limnephilidae	53.3	14.6	7.8
Ceratopogonidae	46.7	4.6	0.5
Copepoda	20.0	1.3	0.4
Sialidae	20.0	.8	36.2

[a]Adults all other taxa consumed as larvae.

POND TEMPERATURE AND DISSOLVED OXYGEN

Pond temperatures from December through May, at 0.3 m of depth, ranged from 4.0 to 15.0°C and in both ponds during December and January moderated between 4.0 and 7.0°C. Inlet water in both ponds was a constant 8.3°C through the winter; however, this warmer water influenced only limited areas in each pond.

Dissolved oxygen measurements ranged from 11.0 to 9.5 mg/L in Pond 1 and from 10.6 to 7.7 mg/L in Pond 2. In both ponds the lower readings came from the deepest areas.

Discussion

Morphometry indirectly affected survival and growth of overwintering juvenile coho, being the singular most apparent difference in the limnology of the study ponds.

General observations revealed that herons and kingfishers frequented both ponds daily and mergansers have occasionally been observed on both ponds. Avian predation is probably the main cause of mortality to pond residents, although mammalian predators have been observed as well. The elongated shape and extensive shallows of Pond 2 allowed

TABLE 6. Frequency of occurrence, numerical and gravimetric composition of major invertebrate taxa in the diet of juvenile coho in Pond 2.

Prey taxa	Frequency of occurrence	Composition	
		Numerical	Gravimetric
Chironomidae	93.3	12.5	1.4
Chironomidae[a]	86.7	55.4	56.0
Baetidae	66.7	20.5	20.8
Dytiscidae	30.0	1.4	8.6
Coenagrionidae	27.7	1.0	1.4

[a]Adults all other taxa consumed as larvae.

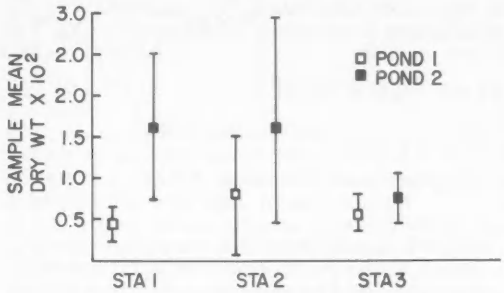

FIG. 2. Benthos sample dry weight (g) compared by station between ponds.

easier hunting for herons and mergansers. Fish in Pond 2 concentrated in a single school beginning in January, perhaps in response to heavy predation, whereas no such behavior was observed in Pond 1.

Lower survival of later immigrants into both ponds might have been associated with successively poorer fish condition as winter progressed. Late arrivals had experienced several severe freshets and a period of low temperatures. Mason (1976) found lipid reserves of underyearling coho of all sizes declining progressively through winter but a more pronounced reduction in the smaller fish. This may in part explain the better survival of the early arrivals as they would have been able to conserve lipid reserves to a greater degree in the benign pond environment.

Because temperatures were nearly identical, superior growth of fish in Pond 2 (nearly twice as great as in Pond 1) appears to be the outcome of greater prey abundance and its exploitation rate.

Abundance of food in these two ponds is, in part, determined by morphometry. Depth restricts the growth of attached aquatic macrophytes in Pond 1, whereas in Pond 2 these plants grow throughout the pond. Aside from providing a high-quality detrital base for insect production (Hodkinson 1975), there is a rich invertebrate fauna directly associated with such aquatic macrophytes (Berg 1950).

Although coho in Pond 2 had eaten larger meals, the more-abundant food base may also have been of higher quality than that in Pond 1 where the fish fed largely from the benthos on encased limnephilid and chironomid larvae. Additionally, if the coho in Pond 1 avoided predators during the winter by staying in the deep part of the pond, this would also have influenced their growth as that area of the pond had the lowest benthos densities.

Implications for Habitat Enhancement

This study demonstrates that survival and growth of juvenile coho overwintering in riverine ponds can be strongly influenced by pond morphometry. These findings suggest that enhancement of winter habitat, such as constructing pond environments or providing access to such areas, should be evaluated more extensively. It may be possible to maximize both survival and growth benefits to overwintering fish by combining the productivity of a shallow pond and the cover aspects of a deeper one in riverine environments.

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BERG, C. O. 1950. Biology of certain Chironomidae reared from *Potamogeton*. Ecol. Monogr. 20(2).

BUSTARD, D. R., AND D. W. NARVER. 1975. Aspects of the winter ecology of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 32: 667–680.

ELLIOTT, J. M. 1977. Some methods for the statistical analysis of samples of benthic invertebrates, 2nd ed. Freshwater Biol. Assoc. Sci. Publ. No. 25.

HODKINSON, I. D. 1975. Energy flow and organic matter decomposition in an abandoned beaver pond ecosystem. Oecologia (Berl.) 21: 131–139.

MASON, J. C. 1976. Response of underyearling coho salmon to supplemental feeding in a natural stream. J. Wildl. Manage. 40: 775–788.

MEEHAN, W. R., AND R. A. MILLER. 1978. Stomach flushing: effectiveness and influence on survival and condition of juvenile salmonids. J. Fish. Res. Board Can. 35: 1359–1363.

PETERSON, N. P. 1982. Immigration of juvenile coho salmon (*Oncorhynchus kisutch*) into riverine ponds. Can. J. Fish. Aquat. Sci. 39: 000–000.

SNEDECOR, G. W., AND W. G. COCHRAN. 1967. Statistical methods, 6th ed. Vol. XIV. Iowa State Univ. Press, Ames, IA. 593 p.

SWANSON, C., AND C. A. SIMENSTAD. 1978. Program FR 306 (Gutbugs). Fish. Anal. Center, Fish. Res. Inst., Univ. Washington, Seattle, WA. 10 p.

Immigration of Juvenile Coho Salmon (*Oncorhynchus kisutch*) into Riverine Ponds[1]

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PETERSON, N. P. 1982. Immigration of juvenile coho salmon (*Oncorhynchus kisutch*) into riverine ponds. Can. J. Fish. Aquat. Sci. 39: 1308 – 1310.

Riverine ponds on the Olympic Peninsula provide important winter refuge for juvenile coho salmon (*Oncorhynchus kisutch*). A total of 9530 juvenile coho migrated into two riverine ponds of the Clearwater River in 1977, principally during fall freshets. Extensive movement by marked fish (as much as 32.6 km downstream) before entering the ponds suggests that a system-wide approach to habitat management is important in maintaining freshwater production potential of large river systems.

Key words: juvenile coho, immigration, winter behavior, migration, freshet, pond

PETERSON, N. P. 1982. Immigration of juvenile coho salmon (*Oncorhynchus kisutch*) into riverine ponds. Can. J. Fish. Aquat. Sci. 39: 1308 – 1310.

Les étangs riverains de la péninsule Olympic constituent un important refuge d'hiver pour les jeunes saumons coho (*Oncorhynchus kisutch*). Un total de 9 530 jeunes coho émigrèrent dans deux étangs riverains de la rivière Clearwater en 1977, surtout au moment des crues automnales. Le fait que des poissons marqués aient entrepris des déplacements d'envergure (jusqu'à 32,6 km en aval) avant de pénétrer dans les étangs donne à penser qu'une approche à la gestion de l'habitat englobant un réseau entier est important pour le maintien du potentiel de production en eau douce des grands réseaux fluviaux.

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THIS paper describes the immigration of juvenile coho salmon (*Oncorhynchus kisutch*) into two riverine ponds on the Olympic Peninsula. Similar upstream migrations into a variety of small stream types during the winter season have been reported from other areas (Skeesick 1970; Elliott and Reed 1974; Bustard and Narver 1975). This behavior suggests that minimization of physical displacement during freshets and avoidance of metabolically expensive stream sites are primary considerations in the selection of winter habitat. My findings show this phenomenon to occur to a far greater extent than has thus far been reported and provide new information about the distance some fish travel before acquiring winter habitat.

Study area — The Clearwater River and two of its riverine ponds comprised the study area (Peterson 1982). During the period of this study discharge in the middle reach of the river ranged from a low of 2.4 m^3/s in August to 404 m^3/s during a November freshet. Outlet streams of Pond 1 and Pond 2 flow 280 and 470 m, respectively, to their confluence with the Clearwater.

Methods — During late summer 409 juvenile coho were captured by electroshocking in the main Clearwater River and cold-branded. After marking, the fish were returned to their specific capture sites which were scattered throughout a 12.6-km reach from Manor Creek to Pond 2, with one location just below Susie Creek (Fig. 1). River sections within this 12.6-km reach were given four-letter codes that indicated the brand used, and the side, position, and orientation on the fish. These codes will be referred to in the Results, and their only significance is to designate the reach of river where fish were marked.

Juvenile coho were collected in traps as they immigrated to the ponds and checked for marks. River discharge and temperature and pond outlet temperature (at the river) were recorded continuously.

Results — Magnitude and timing of immigration — Between August 29, 1977 and March 7, 1978, 3297 and 4029 juvenile coho were caught as they migrated into Pond 1 and Pond 2, respectively. Estimates of total numbers, corrected for periods of trap inoperability, are 4100 and 5430 for Ponds 1 and 2, respectively (Peterson 1982). Over 85% of these fish migrated into the ponds during freshets in October and November. Twenty-four-hour peak catches occurred on November 4 and October 24 at Ponds 1 and 2, respectively. On these dates 212 coho were caught at Pond 1 and 353 at Pond 2. Relatively minor numbers of coho fry (450 in Pond 1 and an undetermined number in Pond 2) migrated into the ponds during the previous spring.

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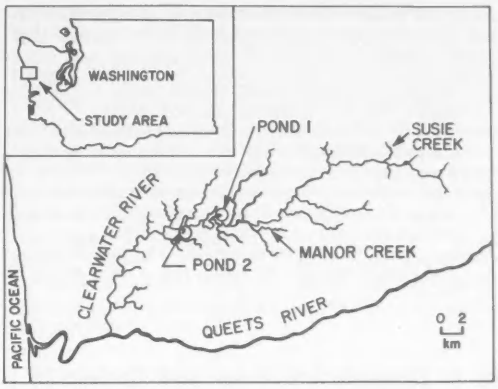

FIG. 1. Location of study ponds on the Clearwater River.

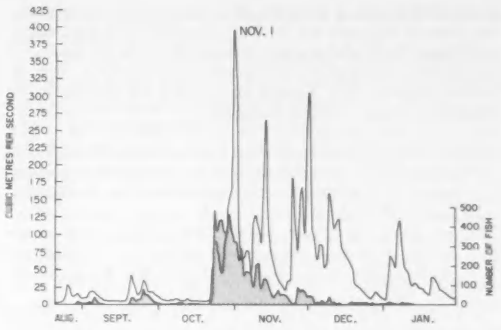

FIG. 2. Plot of the peak daily discharge of the Clearwater River and the total number of fish entering both ponds. Stippled area represents the number of fish and corresponds to the right-hand vertical axis.

TABLE 1. Distance from study ponds upstream to marking sites in the Clearwater River and mark recoveries by pond.

Brand code	No. of marks	km upstream of ponds		Recovery by pond	
		Pond 1	Pond 2	Pond 1	Pond 2
RANV	97	24.9	32.6	3	1
LPSV	16	6.2	13.9	2	0
LPNV	72	4.6	12.3	3	5
LASV	43	1.4	9.1	4	0
LAWV	67	[a]	7.7	1	1
LAEV	34	[a]	5.2	0	7
LANV	80	[a]	1.3	0	12
				13	26
Total	409			39	

[a]Downstream of Pond 1.

Major migration to the ponds was initiated by the first large freshet of the fall on October 23 (Fig. 2). Freshets in August and September, although smaller, also were accompanied by an influx of fish to the ponds.

Summer rearing areas of fall immigrants — Thirty-nine fish marked in the Clearwater River, or 9.4% of the total, were recaptured at the pond traps during the fall immigration. All recaptured fish had moved downstream from their marking location except one. This exception had traveled 0.5 km upstream to Pond 1. The longest distance traveled by a marked fish was 32.6 km (Table 1). This individual was from the RANV group and was branded on September 10 and recaptured in the Pond 2 trap on October 28. Three other fish from this group were captured in the Pond 1 trap, one each on October 31, and November 9 and 19. These three fish had traveled 24.9 km downstream from their summer habitat.

Discussion — The 9530 juvenile coho that assumed winter residence in the Clearwater ponds represent a winter redistribution of juvenile coho far in excess of any reported in the literature. These large-scale migrations probably reflect the relatively large size of the Clearwater system and the position of the ponds below a number of coho-producing tributaries and mainstem-rearing areas. Freshets also occurred prior to the occurrence of water temperatures that initiate winter hiding behavior (Bustard and Narver 1975) and may have caught many juvenile coho in relatively unprotected rearing areas. In addition, I estimate 400 − 500 of the pond recruits could have been fry that emigrated from three tributaries upstream from the ponds and reared in the mainstem as a result of a fry-planting study conducted during the previous spring.

Freshets appeared to induce upstream migration into the ponds in August and September as well (Fig. 2). During the summer, stream-dwelling salmonids normally exhibit home territory behavior (Edmundson et al. 1968; Allee 1974), thus stream flow fluctuations may be the primary influence initiating such movements.

The downstream movements in the present study are the longest recorded for this kind of migration. Juvenile coho entering overwintering streams in the Starrigavin watershed in Alaska are typically recruited from mainstem areas within 0.8 km, although one had traveled 1.6 km (Elliott and Reed 1974). The long distances that some fish traveled in this study may reflect the scarcity of suitable overwinter habitat adjacent to much of the upper Clearwater River mainstem. Nothing is known of the fishes' behavior en route to the ponds. However, some fish marked above Pond 1 went by and were recaptured at Pond 2, indicating that they probably were traveling the margins of the river and forfeited their first opportunity for refuge because they happened to be on the opposite side.

Extensive abandonment of summer-rearing sites and subsequent lengthy relocations to riverine ponds illustrate the complementary nature of widely separated and diverse habitat types in the freshwater production of coho. Arctic char (*Salvelinus alpinus*) have been observed to exhibit similar seasonal habitat dependencies in Alaska (Craig and Poulin 1975). These findings underscore the importance of a system-wide approach to habitat management. Protection of localized summer-rearing habitat alone may not be sufficient to ensure its ultimate fish production, when at a later date, that production may be dependent on entirely different and distant habitat.

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ALLEE, B. J. 1974. Spatial requiremnts and behavioral interactions of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). Ph.D. dissertation, Univ. Washington, Seattle, WA. 160 p.

BUSTARD, D. R., AND D. W. NARVER. 1975. Aspects of the winter ecology of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 32: 667–680.

CRAIG, P. C., AND V. A. POULIN. 1975. Movements and growth of Arctic grayling (*Thymallus arcticus*) and juvenile Arctic char (*Salvelinus alpinus*) in a small Arctic stream. Alaska. J. Fish. Res. Board Can. 32: 689–697.

EDMUNDSON. E., F. E. EVEREST, AND D. W. CHAPMAN. 1968. Permanence of station in juvenile chinook salmon and steelhead trout. J. Fish. Res. Board Can. 25: 1453–1464.

ELLIOTT, S. T., AND R. D. REED. 1974. A study of land-use activities and their relationship to the sport fish resources in Alaska. Alaska Dep. Fish. Game, Study D-1, Job D-1-B. Vol. 15.

PETERSON, N. P. 1982. Population characteristics of juvenile coho salmon (*Oncorhynchus kisutch*) overwintering in riverine ponds. Can. J. Fish. Aquat. Sci. 39: 000–000.

SKEESICK, D. G. 1970. The fall immigration of juvenile coho salmon into a small tributary. Res. Rep. Fish. Comm. Oregon 2: 90–95.

Phosphorus Release Patterns and the Effects of Reproductive Stage and Ecdysis in *Daphnia magna*[1]

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SCAVIA, D., AND M. J. MCFARLAND. 1982. Phosphorus release patterns and the effects of reproductive stage and ecdysis in *Daphnia magna*. Can. J. Fish. Aquat. Sci. 39: 1310–1314.

Rates of continuous phosphorus release by individual *Daphnia magna* (0.3–0.9 mg dry weight) were measured using high performance liquid chromatography components in conjunction with a specially designed incubation flow cell. Within the temporal resolution of the technique (3 min), phosphorus release often appeared pulsed rather than only steady. We found significant variation in release rates among the different stages of an individual's parthenogenetic reproductive cycle. Rates observed for animals carrying more mature embryos were lower than those earlier in the reproductive cycle. Rates of phosphorus release observed at and after ecdysis averaged 6.7 times higher than rates observed at other times.

Key words: phosphorus, excretion, reproductive stage, ecdysis, *Daphnia magna*

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Les taux de mise en liberté continue de phosphore par des *Daphnia magna* individuelles (0,3–0,9 mg de poids sec) ont été mesurés à l'aide de composantes de chromatographie en phase liquide à haute performance, de concert avec une cellule d'incubation avec débit spécialement conçue. Dans les limites de résolution temporelle de la technique (3 min), la mise en liberté de phosphore semble souvent pulsée plutôt que régulière. Parmi les différents stades du cycle reproducteur parthénogène d'un individu, nous observons une variation significative des taux de mise en liberté. Les taux observés chez des animaux portant des embryons plus développés sont inférieurs à ceux dont le cycle reproducteur n'est pas aussi avancé. Les taux de mise en liberté du phosphore observés pendant et après la mue sont en moyenne de 6,7 fois plus élevés que ceux observés à d'autres périodes.

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THE importance of herbivorous zooplankton in controlling available phosphorus concentration in the epilimnion of stratified lakes has been recognized for some time (e.g. Ketchum 1967; Ganf and Blazka 1974; Richey 1979; Scavia 1979; Lehman 1980a, b). Although forms of phosphorus released by zooplankton have been partially characterized (e.g. Pomeroy

et al. 1963; Peters and Lean 1973) and rates of this release have been approximately determined (e.g. Barlow and Bishop 1965; Hargrave and Green 1968; Peters and Rigler 1973; Lehman 1980a, b; Scavia and Gardner 1982), mechanisms controlling phosphorus release have not been elucidated.

We here explore two aspects of phosphorus release by *Daphnia magna*. First, we demonstrate that release of phosphorus is sometimes pulsed. Second, we demonstrate dependence of phosphorus release on the parthenogenetic reproductive cycle of *Daphnia magna*. Animals carrying embryos in late stages of development have relatively depressed rates, whereas animals at and after ecdysis have dramatically increased rates. These results have implications for both the design of experiments and nutrient regeneration in the natural environment.

Materials and methods — Continuous soluble reactive phosphorus (SRP) release rates by individual *Daphnia magna* were measured using a flow-through incubation cell (Gardner and Scavia 1981) in conjunction with high performance liquid chromatographic plumbing. Tygon tubing was substituted for Teflon whenever possible, to minimize phosphorus sorption.

Low-nutrient water (LNW), containing 20 mg $CaCl_2 \cdot 2H_2O$, 10 mg $MgSO_4$, and 20 mg $NaHCO_3$ per litre of distilled, deionized water (Lehman 1980a), and all reagents were pumped through the system with a Technicon proportioning pump. Reagents (Murphy and Riley 1962, as adapted for Technicon AutoAnalyzer) were mixed with water coming from the outlet end of the incubation flow cell in a Technicon AutoAnalyzer manifold. Before reaching the manifold, however, LNW passed through an Altex sample injection valve allowing flow to be diverted from the incubation cell to a bypass loop, to obtain a LNW base line or to change animals. This system is similar to that described by Gardner and Scavia (1981) for measurement of continuous release of ammonia plus primary amines, except nitrogen analyzer and pump are replaced by autoanalyzer components.

Absorbance was recorded with time to provide a continuous record of SRP concentration in the outflowing water. To quantify rates, we replaced the LNW input reservoir by a vial containing standard PO_4 solution prepared with LNW. After a fixed period of time (usually 10 min) the input tube was removed from the standard PO_4 solution, rinsed with distilled, deionized water, and placed back in the original reservoir. An absorbance plateau was observed for the standard solution, followed by a blank base line response after the standard solution had passed through the system.

A stock culture of *Daphnia magna* was maintained in the laboratory under constant fluorescent lighting at 20°C in an aerated tank (ca. 4 L) of filtered Huron River (near Ann Arbor, MI) water. Food supply was maintained through addition of algal cells (*Chlamydomonas reinhardti*) obtained by centrifuging portions of a semicontinuous culture grown on full-strength unbuffered WC medium (Guillard and Lorenzen 1972) without silicate at 20°C under continuous light (~700 lx).

Two experiments were performed. The first examined the kinetic mode (i.e. steady or pulsed) of SRP release and compared results for animals fed algal cells prepared two different ways with respect to phosphorus. The second experiment compared release rates for individuals at different stages in their reproductive cycles.

In the first experiment, animals were maintained initially for ca. 24 h at a high ($>2 \times 10^5$ cell·mL^{-1}) concentration of *Chlamydomonas reinhardti* (~35 μm^3·cell^{-1}). Then animals, for one treatment, were transferred to a culture containing 2×10^5 to 4×10^5 cell·mL^{-1} for 3 h prior to release rate determinations. A second set of animals was transferred to a culture containing 2×10^5 to 4×10^5 cell·mL^{-1} of P-starved algae and also held for 3 h prior to use. P-starved algae were prepared by diluting 400 mL of the original stock algal culture with 1200 mL of WC media lacking P; this was repeated every other day for 6 d prior to their use. Lack of growth following the final dilution indicates that cells were starved for P. A total of 14 animals fed normally cultured cells and 17 fed P-starved cells were analyzed at room temperature (25–27°C).

In the second experiment, three groups of four to eight animals (2.5–2.9 mm long; 0.2–0.7 mg dry weight) were removed at different times from the stock culture. SRP release rates were measured at 20°C during different stages of their reproductive cycles beginning at least 24 h after removal from the stock culture. Individuals were maintained in separate beakers (~100 mL) in which LNW and algal food (*C. reinhardti*) were replaced daily. The concentration of cells in each beaker was maintained in excess of 5×10^5 cells·mL^{-1} (~18.5×10^6 μm^3·mL^{-1}) to ensure maximal feeding rates. The incipient limiting food level for *Daphnia magna* is in the range 2.8×10^6 to 6×10^6 μm^3·mL^{-1} (Kersting and van der Leeuw 1976).

Before release rate measurements, each animal was examined in a depression slide under a dissecting microscope to determine length, measured with an ocular micrometer from tip of the helmet to base of the posterior spine, and reproductive state, including stage and number of embryos present in brood chamber. Embryos were staged as follows: stage I represents eggs prior to any visible differentiation aside from the formation of fat cells; stage II is from differentiation until eyespots become visible; and stage III is from this point until the embryos are released. This classification is similar to that used by Stross et al. (1961) and Edmondson (1955). The short stage between release of young and ecdysis was classified as premolt (P). After this examination (30–90 s) the animal was rinsed in LNW, placed in the incubation flow cell, and the valve switched to direct water past the animal.

SRP release in both experiments was measured for ~30 min to observe release patterns. Recorder response was integrated for the period 5–10 min after beginning in the first experiment and for the period 4–14 min in the second experiment to quantify release rates immediately after the animal was removed from the food. Recall that animals were fed continuously until removed for measuring release rates.

SRP release rates, which in the first experiment were related to wet weight, were converted to dry weight basis by a constant factor (dry weight:wet weight ± SE = 0.100 ± 0.005; n = 47). Wet weights were determined by gently drying each animal with tissue (ca. 3 min) and weighing on a Sartorius six-place balance (precision = ca. 1 μg). Dry weights were determined on animals dried for 48 h at 60°C in preweighed Al planchetts.

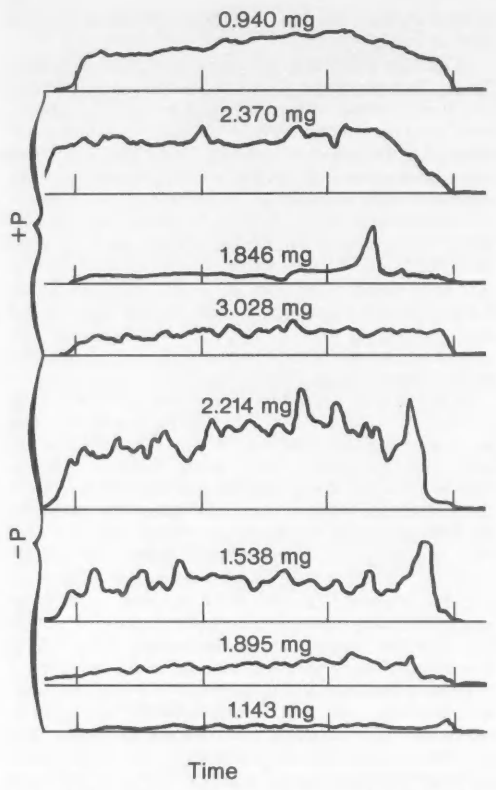

FIG. 1. Representative continuous traces of soluble reactive phosphorus release for 30 min after animals were removed from their food. +P represents animals fed for 3 h on algae grown on full-strength medium. −P represents animals fed for 3 h on P-starved algae. Animal wet weight is indicated on each trace. Height of trace is proportional to SRP release per individual.

Weight-specific release rates in the second experiment were based on a length−weight relationship determined from 30 animals. Each experimental animal's length and dry weight were determined to ensure that it was consistent with the previously determined relationship. Then, the animal's dry weight for each stage of the reproductive cycle was estimated from its length measured at that stage.

Results and discussion — Phosphorus release, in both experiments, was often pulsed. Representative continuous traces of SRP release from the first experiment are shown in Fig. 1. Taylor and Lean (1981) found similar sporadic releases of ^{32}P by the ciliated protozoan, *Strombidium viride*, and the rotifer, *Keratella chochlearis*, although our observed pulsing appears to be at high frequency. These results contrast with the nonpulsed NH_4 release rates observed previously for *D. magna* fed a soyflour/bacteria mixture (Gardner and Scavia 1981). In most cases, pulsing here appeared superimposed upon a base rate; hence it is reasonable to assume

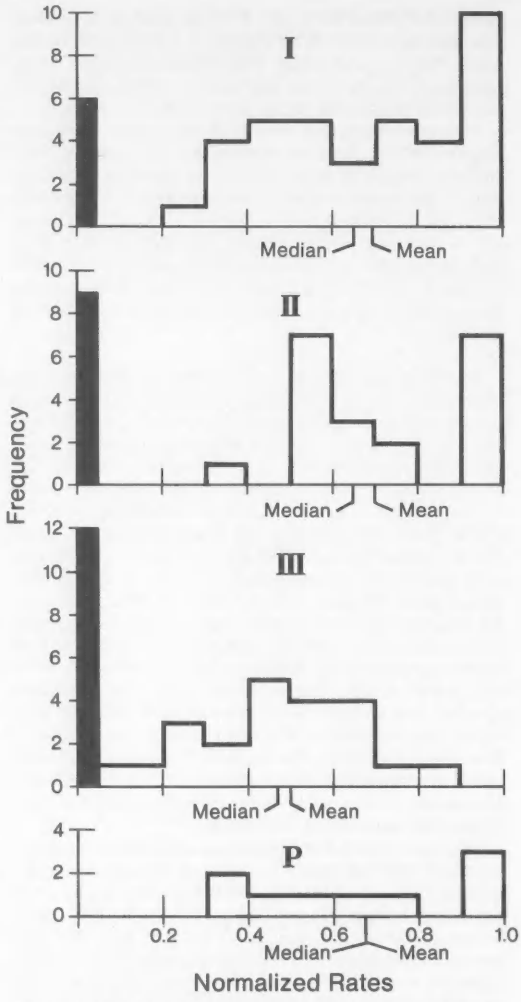

FIG. 2. Histograms of normalized release rates for each reproductive stage. Shaded areas are for measurements below detection. Rates were normalized by dividing each rate by maximum rate obtained for that animal. See text for description of stages I, II, III, and P.

phosphorus excretion is continuous when calculating concentration gradients near zooplankton (e.g. Jackson 1980; Lehman and Scavia 1982a, b). Pulses, possibly from P associated with fecal material as Taylor and Lean (1981) suggest, would provide additional short-term increases in release rates and thus discrete patches of higher concentration. This may be particularly important in cladocerans which produce diffuse feces that break up immediately upon release into the water. The fecal pulses may be most important during periods when animals' feeding rates are high because of increased egestion, and possibly less efficient assimilation, associated

with increased ingestion.

Differences were not discernible betwen 5–10-min rates for animals fed on algae conditioned in two different ways with regard to phosphorus (t-test, two-tailed, 29 df, $P > 0.1$), which suggests that P release kinetics in our experiments were not affected greatly by the way the algae were prepared. Animals fed for 3 h should have replaced the contents of their guts; however, they probably would not have adjusted metabolically to differences in P content of the food.

Mean release rates (± SE), averaged over all animals and reproductive states, for the three groups of animals in the second experiment (1.72 ± 0.222 nmol $P \cdot mg^{-1} \cdot h^{-1}$, $n = 19$; 0.43 ± 0.026, $n = 41$; and 0.29 ± 0.017, $n = 26$) were significantly different ($P < 0.01$, t-test for means with unequal variance estimates). The only known difference among the three groups is their time of removal from mass culture for preconditioning (13 d between first two groups and 19 d between second two groups). Fungal masses were observed in the appendages on some animals from the mass culture near the end of the experiment. Although these were not observed for experimental animals, changing conditions in the mass culture may have been reflected in the decreasing mean rates of these groups. The rates for animals in the first group are similar to those suggested for similar size daphnids by Peters and Rigler (1974) and within the range of those measured for *Daphnia magna* under a different feeding regime (Scavia and Gardner 1982). Because we are concerned here only with differences within the reproductive cycle and to facilitate statistical comparisons, rates for each animal were normalized to the maximum rate measured over all reproductive stages of that animal. Normalized rates (Fig. 2) for animals carrying stage III embryos were statistically lower than those carrying either stage I or stage II embryos (Mann–Whitney U-test, one-tailed, $P < 0.01$) or those in the premolt condition ($P < 0.025$). Differences in normalized rates for premolt, stage I, and stage II animals were not statistically discernible. The ratios of mean normalized rates from stages I, II, and premolt to stage III are, respectively, 1.50, 1.57, and 1.48.

Other physiological and behavioral processes vary with reproductive state. Rates of assimilation (Schindler 1968) and filtration (Nauwerk 1959) are higher for ovigerous than for nonovigerous Cladocera. Filtration rates (Christensen 1973) and carotenoid and hemoglobin content (Green 1956a, 1957) vary with stage of embryonic development in *Daphnia*. Although alteration in filtering appendage movements prior to release of young (Burns 1968) and passage of hemoglobin from blood to eggs prior to molting and extruding eggs into the brood chamber (Green 1956a) suggest mechanisms affecting these processes, mechanisms leading to reduction in phosphorus release for animals carrying more mature embryos are, at this time, unknown.

On four occasions during our experiments and twice during experiments described by Scavia and Gardner (1982), animals in the premolt condition molted in the incubation flow cell during measurement of SRP release. In all cases, SRP release increased dramatically over the rates determined prior to molting. Release rates increased by an average factor of 6.7 (SE = 2.10, $n = 6$, range = 2.7–16.5) over premolt rates. Because, from the above analysis, rates for animals in the premolt condition are not statistically different from the highest nonmolting rates expected during any reproductive cycle, release rates at ecdysis are likely the highest rates the animals attain. Peters and Rigler (1973) estimated, for *Daphnia rosea*, that loss of P at ecdysis due to the carapace alone could account for only a few percent of overall loss; however, they were not able to estimate loss with molting or other fluids. Lee and Buikema (1979) observed molting *Daphnia pulex* to be more sensitive to the effects of chromate during toxicity studies. They suggest that the increased sensitivity may be related to increased chromate uptake during the rapid size increase after molting or to calcium deficiency in the new exoskeleton. Our elevated release rates may be related to permeability of the exoskeleton immediately after molting. The new exoskeleton may be permeable to interior body fluids allowing P to be lost more readily with fluid exchange associated with the dramatic size increase.

To our knowledge, the dramatic increase in phosphorus release at and after ecdysis has not been observed previously, but may have experimental and environmental implications. The higher release rates do not represent discrete injections of P into the surrounding environment, but rather sustained elevated release rates for periods ranging from 15 min to greater than 2 h in our experiments.

A simple, but instructive calculation demonstrates the potential bias introduced if elevated release rates during molting are not considered. Stages I, II, and III each require approximately equal portions of total embryonic development time (Green 1956b). Christensen (1973) observed that the period between release of young and ovulation in the next clutch was approximately equal to that of embryonic development of one stage in *Daphnia magna*. If we assume that P release rates are elevated for only one-half of the time between release of young and ovulation and that the elevated rate is, as we observed, 6.7 times the average rate (R) during stages I, II, and III, then the average rate over the whole reproductive cycle would be

$$\frac{1}{4}\left(3.5R + 0.5 \times 6.7R\right) = 1.7R$$

This rough calculation, showing a 70% difference, demonstrates the impact on inferences drawn from experiments where some of the animals may have molted. If no animals have molted, extrapolation of laboratory estimates to the field may underestimate true flux of P to the water. If an unusually high proportion of the animals molted, true flux may be overestimated.

More important perhaps is the influence these intermittent elevated release rates would have on nutrient heterogeneity. If microenvironments in fact have bearing on algal production and species competition (Turpin et al. 1981) and if zooplankton are important mediators of such heterogeneity (e.g. Goldman et al. 1979; Lehman and Scavia 1982a, b), then focusing elevated release rates into discrete periods of time (i.e. during molt) may also have important implications for algal community production and structure.

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BARLOW, J. P., AND J. W. BISHOP. 1965. Phosphate regeneration by zooplankton in Cayuga Lake. Limnol. Oceanogr. 10(Suppl.): R15–R24.

BURNS, C. W. 1968. Direct observations of mechanisms regulating feeding behavior of *Daphnia*, in lake water. Int. Rev. Gesamte Hydrobiol. 53: 83–100.

CHRISTENSEN, S. 1973. Filtration, ingestion, and egestion of different sized algae by *Daphnia magna* STRAUS. Ph.D. thesis, Yale University, New Haven, CT. 168 p.

EDMONDSON, W. T. 1955. The seasonal life history of *Daphnia* in an arctic lake. Ecology. 36: 439–455.

GANF, G. G., AND P. BLAZKA. 1974. Oxygen uptake, ammonia and phosphate excretion by zooplankton in a shallow equatorial lake (Lake George, Uganda). Limnol. Oceanogr. 19: 313–325.

GARDNER, W. S., AND D. SCAVIA. 1981. Kinetic examination of nitrogen release by zooplankters. Limnol. Oceanogr. 26: 801–810.

GOLDMAN, J. C., J. J. MCCARTHY, AND D. G. PEAVEY. 1979. Growth rate influence on the chemical composition of phytoplankton in oceanic waters. Nature (London) 279: 210–215.

GREEN, J. 1956a. Variation in the hemoglobin content of *Daphnia*. Proc. R. Soc. London Ser. B 145: 214–232.

1956b. Growth, size, and reproduction in *Daphnia* (Crustacea; Cladocera). Proc. Biol. Soc. London 126: 173–204.

1957. Carotenoids in *Daphnia*. Proc. R. Soc. London Ser. B 147: 392–401.

GUILLARD, R. R., AND C. J. LORENZEN. 1972. Yellow-green algae with chlorophyllide c. J. Phycol. 8: 10–14.

HARGRAVE, B. T., AND G. H. GREEN. 1968. Phosphorus excretion by zooplankton. Limnol. Oceanogr. 13: 332–342.

JACKSON, G. A. 1980. Phytoplankton growth and zooplankton grazing in oligotrophic oceans. Nature (London) 284: 439–441.

KERSTING, K., AND W. VAN DER LEEUW. 1976. The use of the Coulter Counter for measuring the feeding rates of *Daphnia magna*. Hydrobiologia 49: 233–237.

KETCHUM, B. H. 1967. Regenerations of nutrients by zooplankton. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 153: 142–147.

LEE, D. R., AND A. L. BUIKEMA JR. 199. Molt-related sensitivity of *Daphnia pulex* in toxicity testing. J. Fish. Res. Board Can. 36: 1129–1133.

LEHMAN, J. T. 1980a. Release and cycling of nutrients between planktonic algae and herbivores. Limnol. Oceanogr. 25: 620–632.

1980b. Nutrient recycling as an interface between algae and grazers in freshwater communities, p. 251–263. *In* W. C. Kerfoot [ed.] Evolution and ecology of zooplankton communities. New England Press, Hanover, NH.

LEHMAN, J. T., AND D. SCAVIA. 1982a. Microscale patchiness of nutrients in plankton communities. Science (Washington, D. C.). 216: 720–721.

1982b. Microscale nutrient patches produced by zooplankton. Proc. Natl. Acad. Sci. 79(16).

MURPHY, J., AND J. P. RILEY. 1962. Determination of phosphate in natural waters. Anal. Chem. Acta 27: 31–36.

NAUWERK, A. 1959. Zur bestimmung der filtrierrate limnischer Planktontiere. Arch. Hydrobiol. (Suppl.) 25: 83–101.

PETERS, R. H., AND D. R. S. LEAN. 1973. The characterization of soluble phosphorus released by limnetic zooplankton. Limnol. Oceanogr. 18: 270–279.

PETERS, R. H., AND F. H. RIGLER. 1973. Phosphorus release by *Daphnia*. Limnol. Oceanogr. 18: 821–839.

POMEROY, L. R., H. M. MATHEWS, AND H. S. MIN. 1963. Excretion of phosphate and soluble organic phosphorus compounds by zooplankton. Limnol. Oceanogr. 8: 50–55.

RICHEY, J. E. 1979. Patterns of phosphorus supply and utilization in Lake Washington and Findley Lake. Limnol. Oceanogr. 24: 906–916.

SCAVIA, D. 1979. Examination of phosphorus cycling and control of phytoplankton dynamics in Lake Ontario with an Ecological Model. J. Fish. Res. Board Can. 36: 1336–1346.

SCAVIA, D., AND W. S. GARDNER. 1982. Kinetics of nitrogen and phosphorus release by *Daphnia magna*. Hydrobiologia. (In press)

SCHINDLER, D. W. 1968. Feeding, assimilation, and respiration rates of *Daphnia magna* under various environmental conditions and their relation to production estimates. J. Anim. Ecol. 37: 369–385.

STROSS, R. G., J. C. NEESS, AND A. D. HASLER. 1961. Turnover time and reproduction of planktonic *Crustacea* in limed and reference portions of a bog lake. Ecology 42: 237–245.

TAYLOR, W. D., AND D. R. S. LEAN. 1981. Radiotracer experiments on phosphorus uptake and release by limnetic microzooplankton. Can. J. Fish. Aquat. Sci. 38: 1316–1321.

TURPIN, D. H., J. S. PARSLOW, AND P. S. HARRISON. 1981. On limiting nutrient patchiness and phytoplankton growth: a conceptual approach. J. Plankton Res. 3: 421–431.

Capacity Reduction on Norwegian Industrial Fisheries[1]

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Catch and processing capacity in Norwegian industrial fisheries may be extensively

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reduced without affecting gross revenue. A linear programming model for maximizing annual revenue in the Norwegian industrial fisheries was formulated. The main purpose of the modeling effort was to determine the minimal size of the fleet and the industry. The constraints of the model are on catch and on capacity in fishing, transporting, and processing.

Key words: linear programming, capacity reduction.

FLÅM, S. D., AND S. STORØY. 1982. Capacity reduction on Norwegian industrial fisheries. Can. J. Fish. Aquat. Sci. 39: 1314 – 1317.

La capacité de capture et de transformation dans les pêches industrielles norvégiennes pourrait être considérablement réduite sans que le revenu brut en soit affecté. Nous avons construit un modèle de programmation linéaire visant à porter au maximum le revenu annuel de ces pêches. L'objectif principal du modèle est de déterminer l'ampleur minimale de la flottille et de l'industrie. Les contraintes du modèle portent sur les prises et la capacité de pêche, de transport et de transformation.

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THE economic theory of common property renewable resource utilization (Gordon 1954) predicts an equilibrium of resource and effort that in the profitable case is likely to be marked by a relatively large amount of effort, depressed stocks, and a low sustainable yield. The present state in the Norwegian industrial fisheries is very much in concordance with this picture. Some 450 vessels, recruited in a regime with free entry, exploit pelagic fish populations in the North Sea and the Barents Sea. They transport the catch to factories spread out along almost the entire Norwegian coast where it is processed mainly into fish meal and oil.

The current management problem concerns overcapacity. This justifies a regulated exploitation. The main purpose of the present model is to determine minimal catch capacity subject to speficied quotas on harvest; the time horizon is 1 yr. The model we present here is a multispecies, multiboat-type, and multifactory model. We allow the vessels to be unequal in size, and we use various speeds and fishing gear. The total quotas on the diverse species may be distributed (as a set of constraints) across time, fishing grounds, vessel groups, and possibly factories. Some fishing gear may be restricted to certain areas. We assume that the catch is to be transported from the fishing ground to the processing factories by the vessels themselves.

Throughout this paper product prices are exogenous and fixed. This reflects the fact that the industry is very much a pricetaker in a competitive world market. Although it would be possible to recognize the existence of multiple objectives (Mathiesen 1979), the criteria utilized by us is the one-dimensional profit of the catch sector of the industry.

The main question addressed is as follows: What will be the most profitable fleet structure? As a by-product, we are able to spot redundancies in the processing capacity. Next, we provide some background information, then we introduce the linear programming model, and present some results. Finally we discuss some limitations and virtues of the model.

Background information — Structural problems of the industry arise because of instability in the level and the composition of catch. Some stocks have been almost depleted while the exploitation of others is of relative recent date. We ignore population dynamics altogether and simply assume that the quotas reflect sustainable yield.

As a brief system description we emphasize that fishing grounds are distributed across a vast area. The capelin fisheries in the Barents Sea are most important; the relative importance of the fisheries in the North Sea has declined. This shift in effort northwards has not been accompanied by a corresponding relocation of processing capacity. Still, there is huge overcapacity south of Nordland while the seasonal variability of landings makes processing capacity in northern Norway effectively constraining the fisheries during two periods of the years: the winter and summer fisheries in the Barents Sea. Then large quantities of catch are transported southwards by the fishing vessels themselves.

The major problem at present concerns overcapacity and economic deficits. This justifies a regulated exploitation and subsidies. The number of vessels has declined and their average cargo capacity has increased during the last decade reflecting economies of scale. Although a licensing scheme was installed in 1973 for the purpose of restricting entry, total cargo capacity kept rising for a long time. Active vessels were enlarged and in fact some new ones were given admittance.

Model overview — The basic decision variables are x_{tvsaf}, the number of trips in time period t completed by vessel group v bringing species s, caught at the fishing area a, to factory f. By a trip is meant a round trip. There are five different vessel groups, and six different species each harvested at several particular grounds. Geographically, concentrated factories are aggregated into a single one leaving 15 factories altogether. The number of time periods is a matter of decision. We used four time periods. The objective function of the model is

$$\sum_{tvsaf} c_{tvsaf}\, x_{tvsaf}$$

which is to be maximized. c_{tvsaf} is the contribution to profit in time period t by "one v-catch" of species s taken at a and transported to f. Constraints of the model are

$$\sum_{tvsaf} a_{tvsaf}\, x_{tvsaf} \leq b_i,\ i = 1, \ldots, m$$

where a_{tvsaf} represents the resource requirements (substitution rates) for each of the relevant trips and b_i is the corresponding resource limit. There are three families of constraints of the model: those concerning fleet capacities, capacities at the factories, and finally catch limits. The processing and storage capacity puts an upper limit on the quantity received at a factory. What is not processed during a period must be stored. Only few species can be stored. For most species there are quotas on total catch. In any case total catch is distributed across time and fishing grounds. This is done by requiring s-catch on ground a in period t to make up an acceptable percentage of total s-catch. One may also consider a distribution of s-catch on vessel groups or factories. Parameters of the model are as follows:

q_{tvs} = the cargo capacity of a vessel of type v in period t when transporting species s (note that even if the physical capacity of a vessel is constant, restrictions like maximal catch quotas on each trip may be introduced).

p_{ts} = the price paid for species s in period t. Then the gross value of a v-load of species s in period t is $p_{ts}q_{tsv}$. To compute the net value, costs must be deducted.

k_{vsaf} = the cost for a trip by a vessel v to catch species s on field a and deliver it to factory f (a trip from a to f will be calculated as a round trip).

Then the profit contribution of such a trip becomes

$$p_{ts}q_{tvs} - k_{vsaf} \; (= c_{tvsaf}).$$

Costs are mainly due to consumption of labor time and fuel. These components depend oppositely on speed.

Q_s = total quota for species s.

α_{tsa} = percentage of Q_s caught at a in period t.

Some results using the model — Suppose the following quotas are all to be caught by the purse seiner fleet:

	Millions of hL	Price per hL,[a] N.kr.[b]
Winter capelin (*Mallotus villosus*)	7	37.54
Summer capelin in the Barents Sea	4	50.43
Capelin at Jan Mayen	1	50.43
Sprat	0.6	65.04
Mackerel	0.4	77.56
Blue whiting	1.5	27.15
Sum	14.5	

[a]We have adhered to the rather non-standard Norwegian practice of measuring catch of industrial fish in hectolitres (hL).

[b]N.kr. represents Norwegian Kroner.

Then the summer capelin fisheries in the Barents Sea requires the most capacity. This is the capacity determining season.

The minimal fleet together with sensitivity analysis would be as follows:

Vessel group by cargo capacity (hL)	0–3999	4000–5999	6000–7999	≥8000
Available fleet in 1979	31	68	49	44
Number of necessary vessels, basic run when each trip in the summer capelin fisheries requires 60 h of catch time, the quota is 4 million hL, and the duration 8 wk	0	0	34	44
when catch time is 72 h/trip	0	0	39	44
when catch time is 80 h/trip	0	0	44	44
when the summer capelin quota is 4.5 million hL	0	0	46	44
when the summer capelin fisheries last 7.5 wk	0	0	49	44

It is not surprising that a rather remarkable pure profit arises as the fleet is reduced towards minimum.

After capital costs, depreciation, fuel, and labor have been fully paid for (alternative cost), what remains is the pure profit. This is shown for different fleets as follows:

	Fleet in 1979	Alternative fleets 1	2	3	4	5	6	7
Number of vessels 0–3999 hL	31	21	11	0	0	0	0	0
Number of vessels 4000–5999 hL	68	58	48	38	28	18	8	0
Number of vessels 6000–7999 hL	49	49	49	49	49	49	49	34
Number of vessels ≥8000 hL	44	44	44	44	44	44	44	44
Pure profit (million N.kr.)	−225	−162	−98	−32	7	45	84	185
Catch capacity: summer capelin when the duration of the fishery is 9 wk	6.62	6.32	6.02	5.70	5.48	5.29	5.08	4.45
winter capelin	7.51	7.18	6.83	6.49	6.29	6.00	5.79	4.97 11.72

A reduced fleet does not need subsidies under a realistic set of price and cost assumptions. It is profitable even if it is required to maintain its present employment. With a minimal fleet one may worry about the risk of not being able to catch randomly increased quotas. This risk seems to be totally negligible in periods other than the effectively constraining summer season. For the summer capelin fisheries, however, one has first to identify the objective nature of random variation. Can part of the quota be transferred to the winter fisheries? Can the duration of summer fisheries be prolonged? If the answer is yes to one or both of these questions, it appears that the system is able to cope rather easily with the problem of genuine randomness. In any case the fleet would be able to pay user cost to the society (the resource owner) and not continue to consume subsidies.

By experimenting with production capacities in the processing industry we reveal that capacity should be maintained in northern Norway, taken away in the middle region, and reduced by 40% in the southern part. These results were presented to the Norwegian Department of Fisheries for planning purposes.

Discussion of the model — Much of the theoretical work in fisheries economics has been aimed at identifying and characterizing dynamically optimal harvest strategies. Issues have also included the existence and properties of steady-state equilibria, the design of necessary regulations, and economic conditions resulting in stock extinction. The most recent trend in the theoretical literature is to account for uncertainty in the population dynamics.

Most models are highly aggregated, however, both from a biological and an economical point of view. In this study the objective was to give a fairly detailed assessment of catch capacity and profit in the Norwegian industrial fisheries and to optimize the industrial structure. We wanted to account relatively accurately for revenue and cost in the short run, and to give a rather minute description of the fleet's activity choice. This compelled us to contend with a static optimization and to ignore population dynamics and intertemporal catch allocation altogether. One sees that our focus is on regulated equilibria. Admittedly, the concept of steady state has recently undergone several subtle elaborations in the economic literature. It would be interesting to allow the annual quotas to be random variables with stationary distributions.

The LP model as presented here gives of course in many ways a primitive picture of the real world. We mention a few limitations: (a) the costs need not be linear, (b) stochastic effects are not considered, (c) maximization of net revenue is not the only objective to be considered (see Mathiesen 1979). We do not expect nonlinearities and randomness to cause severe complications or invalidate our conclusions. However, as with other linear models we also have the "all-or-nothing" effect (or the "bang−bang" effect) with this LP model, giving solutions that in many respects are politically infeasible. For example, the model will activate some vessels completely while other vessels are completely unemployed. This effect can be reduced by introducing an entropy constraint (Erlander 1979). Experiments with this have not been undertaken. Stochastic effects may complicate the problem. When the technological parameters a_{rvsaf} are random, the induced probability distribution of the maximum profit is not well behaved. In particular, it is well known that its mean generally will not equal the profit obtained by solving the model with means of the a_{rvsaf}. A related complication for problem formulations using means is that the optimal solution will be feasible only with some probability. Insight may be gained in the particular problem by running the LP several times each time sampling the parameters from their distributions. Uncertainty is greatest about Q_s and q_{rvs}. Afterwards, statistical analysis of the output may be performed (Gaither 1980).

In spite of the limitations and deficiencies mentioned, we believe the model gives important answers to questions regarding capacity adaptation in industrial fisheries. On long-run investment decisions it also has something to offer by tracing out the profit curve as a function of aggregate capacity. With an extended time horizon, however, randomness and population dynamics have to be considered (Anderson and Ben-Israel 1979). In any case the LP-calculated short-term, optimal revenue can be used as input in a multistage decision process. With a specified discount rate and given system dynamics, the long-term problem is to choose a harvesting strategy maximizing the present value of the optimal net revenue flow. Thus the multistage problem will be to select over time the constraint levels given exogeneously to the one-stage problem we studied.

ANDERSON, L. G., AND A. BEN-ISRAEL. 1979. Modelling and simulation of interdependent fisheries and optimal effort allocation using mathematical programming. *In* K. B. Hailey [ed.] Proc. NATO Symposium on Applied Operations Research in Fisheries, Trondheim. University of Birmingham, U.K.

ERLANDER, S. 1981. Entropy in linear programs. Math. program. 21: 137−151.

GAITHER, N. 1980. A stochastic constrained optimization model for determining commercial fishing seasons. Manage. Sci. 26: 143−154.

GORDON, H. S. 1954. The economic theory of a common property resource: The fishery. J. Polit. Econ. 62: 124−172.

MATHIESEN, L. 1979. A multi-criteria model for assessing industrial structure in the Norwegian fishmeal industry. *In* K. B. Hailey [ed.] Proc. NATO Symposium on Applied Operations Research in Fisheries, Trondheim. University of Birmingham, U.K.

Blood Protozoa as an Aid for Separating Stocks of Greenland Halibut, *Reinhardtius hippoglossoides*, in the Northwestern Atlantic[1]

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Samples of subadult Greenland halibut, *Reinhardtius hippoglossoides*, from several northwest Atlantic locations, the Gulf of St. Lawrence, and Fortune Bay, an inlet on the south coast of Newfoundland, were examined for the prevalence of two blood protozoa. Because prevalence of infection varied widely, the data were analyzed using the general least squares analysis of fitting constants on logit values. Trypanosome and piroplasm infections in samples from Davis Strait, NAFO divisions 2G–2H and div. 3L, were mostly similar, but differed significantly from div. 2J–3K. Trypanosome infections in samples from the northwest Atlantic locations were significantly higher than in the Gulf of St. Lawrence and Fortune Bay. Piroplasm infections were significantly higher in samples from Fortune Bay than in the Gulf of St. Lawrence. The results suggest that Greenland halibut from Davis Strait, div. 2G–2H and div. 3L, are composed of one stock complex, while fish from div. 2J–3K represent an isolated group or most probably a cline between areas. Greenland halibut from the Gulf of St. Lawrence and Fortune Bay appear to represent distinct stocks.

Key words: blood protozoa, trypanosome, piroplasm, Greenland halibut, stock separation, northwestern Atlantic

KHAN, R. A., M. DAWE, R. BOWERING, AND R. K. MISRA. 1982. Blood protozoa as an aid for separating stocks of greenland halibut, *Reinhardtius hippoglossoides* in the northwestern Atlantic. Can. J. Fish. Aquat. Sci. 39: 1317–1322.

Des échantillons de flétans du Groenland subadultes (*Reinhardtius hippoglossoides*) provenant de plusieurs endroits de l'Atlantique nord-ouest, du golfe du Saint-Laurent et de la baie de Fortune, une baie de la côte sud de Terre-Neuve, ont été examinés en vue d'y détecter la présence de deux protozoaires du sang. À cause de la grande variation d'incidence, la méthode des moindres carrés d'ajustement de constantes aux valeurs logit a été utilisée dans l'analyse des données. Les infestations de trypanosomes et pyroplasmes sont essentiellement identiques dans les échantillons provenant du détroit de Davis, div. 2G–2H et div. 3L de l'OPANO, mais diffèrent de façon significative de celles des div. 2J–3K. Les infestations de trypanosomes dans les échantillons de sites de l'Atlantique nord-ouest sont nettement plus élevées que dans ceux du golfe du Saint-Laurent et de la baie de Fortune. Les infestations de pyroplasmes sont significativement plus élevées dans les échantillons de la baie de Fortune que dans ceux du golfe du Saint-Laurent. Ces résultats donnent à penser que le flétan du Groenland du détroit de Davis, div. 2G–2H et div. 3L, représente un complexe de stocks, alors que les poissons de la div. 2J–3K sont un groupe isolé ou, plus probablement, un cline entre régions. Le flétan du Groenland du golfe du Saint-Laurent et de la baie de Fortune semble appartenir à des stocks distincts.

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GREENLAND halibut (*Reinhardtius hippoglossoides*) are widely distributed in the north Atlantic and Pacific oceans but restricted to the arctoboreal region by temperature (Hubbs and Wilimovsky 1964). This species constitutes a major component of the commercial, groundfish fishery in the Newfoundland–Labrador area (Templeman 1970, 1973; Lear 1970a; Bowering and Pitt 1975; Bowering 1978a, b). Inshore landings are composed mainly of subadult fish. Greenland halibut apparently spawn during winter–spring in the deep, warm waters of Davis Strait (Smidt 1969). The pelagic eggs and larvae from deepwater spawning are carried by the Labrador current southwards into coastal areas of Newfoundland–Labrador and the northern Grand Bank (Templeman 1973; Bowering 1980a). The fish therefore spend most of their subadult life in coastal and more southern areas and migrate subsequently offshore and northward into deep water for reproductive purposes. It is this movement that complicates the identity of stocks. Some of the conventional methods used in stock discrimination, such as meristics, food, growth rate, tagging, etc., have provided valuable information (Lear 1970a, 1970b; Lear and Pitt 1975; Templeman 1970, 1973; Bowering 1978b). However, additional methods for verification are required. Parasites have been used previously as biological tags (Margolis 1963; Templeman et al. 1957; Templeman and Squires 1960; Templeman and Fleming 1963). A recent study suggested that stocks of Atlantic cod (*Gadus morhua*) could be identified using the blood parasite *Trypanosoma murmanensis* as an indicator (Khan et al. 1980b). Because Greenland halibut are susceptible to two blood protozoa, viz., a trypanosome, *T. murmanensis* and a piroplasm, *Haemohormidium terraenovae* (Khan et al. 1980a), this study was undertaken to ascertain their significance in stock separation.

Materials and methods — The program was designed to sample Greenland halibut from several geographical areas. Fish were collected from Davis Strait to the south and west coasts of Newfoundland (Fig. 1) during 1978–80 by Canadi-

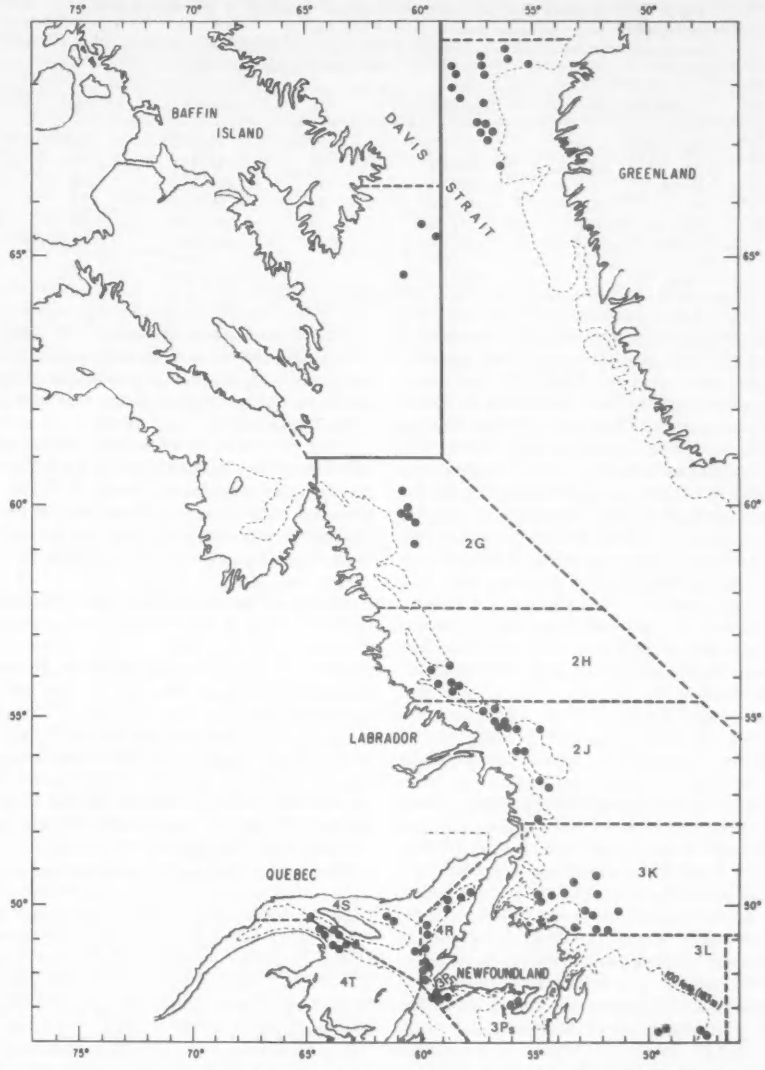

FIG. 1. Sampling localities (solid black circles) from which Greenland halibut were examined for the presence of blood parasites.

an research vessels using an otter trawl with a small mesh liner. Water temperatures varied from 1.0 to 3.0°C at depths varying from 300 to 610 m. We recorded the total length of all fish (32–76 cm), sex, and maturity. All fish were immature. We prepared thick and thin blood smears as described previously (Khan et al. 1980a), from blood removed by a heparinized syringe and needle from the dorsal aorta. Thick smears were incubated at 60°C for 30 min and stained with Giemsa while thin smears were fixed in methanol and then stained. Slides were examined for periods up to 20 min, using a 20 × objective for thick and a 100 × for thin smears.

Statistical analysis was done by R.K.M., who also wrote the computer program for it in Fortran IV and supported under IBM/370. The analysis was adopted from Snedecor and Cochran (1967, Chap. 16) and Harvey (1975). Individual samples within each division were combined. The data in Table 1 was classified two ways, by six rows (NAFO divisions) and two columns (parasites), with n_{ij} fish examined

TABLE 1. Prevalence of trypanosome and piroplasm infections in Greenland halibut in the Newfoundland–Labrador area.

NAFO division	No. infected/No. examined			
	Trypanosome	%	Piroplasm	%
Davis Strait	23/102	23	77/102	76
2G–2H	84/260	32	184/232	79
2J–3K	70/339	21	299/338	89
3L	36/100	36	58/81	72
3Pn–4R–4S–4T	11/140	8	81/139	58
Fortune Bay (3Ps)	6/156	4	118/146	81
Total	230/1097		817/1038	

in the cell of the ith row and jth column. The purpose of analysis was twofold: firstly, to examine variations in prevalence of each blood protozoan in the NAFO divisions (main effects), and secondly to investigate if differences in prevalence of the two protozoa varied from one NAFO division to another (interaction effects). Because there were disproportionate cell frequencies (Table 1), the exact test of the null hypothesis that interactions are absent was done by the general least squares analysis of fitting constants. For data on continuous measurements the model for analyzing two-way classifications defined by r rows and c columns, assuming no interactions, may be given as, $\bar{X}_{ij\cdot} = \mu + \alpha_i + \beta_j + \bar{\epsilon}_{ij\cdot}$; $= i = 1, \text{-----}, r; j = 1, \text{-----}, c$, where $\bar{X}_{ij\cdot}$ is the cell mean of n_{ij} observations, and $\bar{\epsilon}_{ij\cdot}$ is assumed to be normally distributed, with mean zero and variance σ^2/n_{ij}. As an intermediate step in calculations, the method provides the 'most powerful' test of the null hypothesis that interactions are zero. If this hypothesis is rejected by the data, further calculations are stopped as the main effects, and the corresponding sum of squares may be biased. Examination of the row effects should then be done separately in each column.

From the viewpoint of theory, the analysis of proportions p_{ij} (= number of infected individuals/total number of individuals examined in the ith row and jth column) is more difficult than that of normally distributed continuous variables. One may consider p_{ij} as a normally distributed variable, with variance $= p_{ij}(1 - p_{ij})/n_{ij}$ and replace $\bar{X}_{ij\cdot}$ by p_{ij} and n_{ij} by its weight w_{ij} which $= n_{ij}/p_{ij}(1 - p_{ij})$. However, we preferred to transform p_{ij} to its logit Y_{ij}, for the following reasons. Because p_{ij} covers a wide range, viz., 4–89% (Table 1), row and column effects are more likely to be additive on a logit scale than on the untransformed (p) scale. In the logit scale row and column, effects may be additive as opposed to the p scale where interactions shown by the same data may just be a consequence of the scale.

Logit Y_{ij} ($i = 1, \text{-----}, 6; j = 1, 2$) was calculated as:

$$Y_{ij} = 1_n[(g_{ij} + 0.5)/(n_{ij} - g_{ij} + 0.5)]$$

with weight $w_{ij} = (g_{ij} + 0.5)\cdot(n_{ij} - g_{ij} + 0.5)/(n_{ij} + 1)$ assigned to this logit, where 1_n denotes the log to base e and g_{ij} is the number of infected fish in the cell of the ith row and jth column. In the analysis of the least squares model, restrictions imposed were $\sum_{a=1}^{6} a_{ij} = \sum_{j=1}^{2} b_{ij} = 0$.

The interaction sum of squares was significant (χ^2 test, $P < 0.005$). Individual deviations between observed (Y_{ij}) and expected ($\hat{Y}_{ij}$) values were also examined. Table 2 gives these deviations and the values of their contributions, $W_{ij}(Y_{ij} - \hat{Y}_{ij})$, to the interaction χ^2.

There were large variations in deviations and in their contributions to the interaction χ^2 (Table 2). This became more obvious when paired comparisons of NAFO divisions were made and tested by χ^2. As interactions for the two-way classification were significant, these paired comparisons were made for each parasite separately (Table 3).

Results — The mean prevalence of trypanosome and piroplasm infections in Greenland halibut originating from NAFO divisions is shown in Table 1. Trypanosome prevalences were greater (21–36%) among fish taken in Davis Strait and through 2G–2H, 2J–3K, and 3L than in the Gulf of St. Lawrence (div. 3Pn–4R–4S–4T, 8%) or in Fortune Bay (div. 3Ps, 4%). There were no apparent differences pertaining to sex or total length of the fish. Piroplasm infections while high (72–89%) along areas north and east of Newfoundland (Davis Strait, div. 2G–2H, 2J–3K, and 3L) were apparently similar (81%) in fish from Fortune Bay but lowest (58%) in the Gulf of St. Lawrence.

Statistical analysis of the data indicated similarities be-

TABLE 2. Values of deviations $Y_{ij} - \hat{Y}_{ij}$ (upper figure) and their contributions $W_{ij}(Y_{ij} - \hat{Y}_{ij})$ (lower figure) to the interaction χ^2. See Table 3.

NAFO division	Parasite	
	Trypanosome	Piroplasm
Davis Strait	0.1508	−0.1425
	0.4124	0.3899
2G–2H	0.2215	−0.3295
	2.8032	4.1708
2J–3K	−0.2857	0.4574
	4.5599	7.3018
3L	0.4779	−0.6644
	5.3233	7.4012
3Pn–4R–4S–4T	−0.0986	0.0306
	0.1027	0.0319
Fortune Bay	−1.5288	0.4146
	14.5639	3.9499

TABLE 3. Paired comparisons of NAFO divisions. Tests above the diagonal line for trypanosome and those below it for piroplasm. (ns stands for not significant ($P > 0.05$); *, **, ***, **** indicate significance at probability levels of 5%, 2.5%, 1%, and 0.5%, respectively.)

NAFO division	Davis	2G−2H	2J−3K	3L	3Pn−4R−4S−4T	Fortune Bay
Davis Strait		ns	ns	*	****	****
2G−2H	ns		****	ns	****	****
2J−3K	****	****		****	****	****
3L	ns	ns	****		****	****
3Pn−4R−4S−4T	***	****	****	ns		ns
Fortune Bay (3Ps)	ns	ns	*	ns	***	

tween fish sampled from Davis Strait and NAFO div. 2G−2H with respect to both parasitic infections (Tables 2 and 3). The infection in fish in div. 3L while similar to that of div. 2G−2H was significantly different from the Davis Strait (5% level) sample for trypanosome but not for piroplasm infections. Each of the three NAFO div. 2J−3K, 3Pn−4R−4S−4T and Fortune Bay differed significantly from every other NAFO division.

The Fortune Bay sample differed from all Atlantic areas for trypanosome infections at the 0.5% level but piroplasm infections in three of the four areas (except NAFO div. 2J−3K) were similar. As a result of the low prevalence of trypanosome infections, no differences occurred between the Fortune Bay and Gulf of St. Lawrence samples, but they were significantly different (0.5% level) from each other for piroplasm infections.

Discussion — Studies on Greenland halibut suggest that a number of stocks exist in the northwest Atlantic prior to migration at maturity. Chumakov (1975) and Zilanov et al. (1976) have proposed that Greenland halibut in the area extending from northwestern Greenland south to Grand Bank is a single interbreeding stock complex. Apparently isolated stocks occur in the Gulf of St. Lawrence and in southwest Newfoundland in Fortune−Hermitage bays (Lear 1970a; Lear and Pitt 1971; Templeman 1973; Bowering 1978a, 1980a). In fecundity−length relationship studies, Bowering (1980b) noted significant differences between Greenland halibut samples originating from southern Labrador and the northeast Newfoundland shelf (div. 2J−3K) and the Gulf of St. Lawrence. Fish from the latter displayed greater fecundity, which he attributed to maturity at an earlier age. The presence of mature and prespawning Greenland halibut in the Gulf of St. Lawrence, moreover, leads to the view that these fish spawn in this area and represent a stock distinct from the northwestern Atlantic stock complex. Information in support of the Fortune−Hermitage fish as a separate stock is scanty as mature females are rarely taken in this area. However, virtual absence of Greenland halibut from the area extending from the western extremity of Hermitage Bay to the Port-aux-Basques region suggests two separate populations. The possibility of isolation via the shallow Avalon Channel from the east coast complex is apparent as shallow warmer water tends to reduce the dispersal of larval and juvenile Greenland halibut (Templeman 1973).

Our results suggest that Greenland halibut from Davis Strait, div. 2G−2H and div. 3L (northern Grand Bank), represent one stock complex. The sample from southern Labrador and the northeast Newfoundland shelf (div. 2J−3K) is different from the aforementioned regions and might represent an isolated population or most probably a cline between areas. Moreover, samples of Greenland halibut from Bonavista and Trinity bays (div. 3L) suggest similarities to the southern Labrador sample (Khan unpublished data). The Gulf of St. Lawrence sample is, however, distinct from all samples north and east of Newfoundland and most probably represents a separate stock as implied by Bowering (1980b). Trypanosome prevalences in the Gulf and Fortune Bay samples are too low for use as valid comparisons. However, significant differences were observed with piroplasm infections and it appears, on this basis, that the Fortune Bay fish are distinct from those in the Gulf of St. Lawrence. Moreover, recent tagging studies (Bowering unpublished data) suggest that Greenland halibut tagged in Fortune Bay do not move out of this area. The Fortune Bay sample, however, is only partially distinct (based on trypanosome prevalence) from that of Davis Strait, div. 2G−2H and 3L, whereas it is significantly different from the southern Labrador sample. The higher prevalence of codworm, *Phocanema decipiens*, in Greenland halibut taken from the Gulf of St. Lawrence and its virtual absence in fish from Fortune Bay is further evidence that little mixing occurs between the two groups (Khan unpublished data). Templeman et al. (1957) also reported that prevalences of *P. decipiens* were higher in four species of fish occurring in the Gulf of St. Lawrence than in other areas. Data from recent biochemical studies provide additional evidence in support of our conclusions on Greenland halibut (Fairbairn 1981). Analysis of allele and genotype frequencies in Greenland halibut suggests that fish originating from the northwestern Atlantic Ocean constitute a genetically homogeneous stock and differ from those which occur in the Gulf of St. Lawrence.

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BOWERING, W. R. 1978a. The exploitation of the Greenland halibut stock complex of ICNAF Subarea 2 and Divisions 3KL. ICNAF Res. Doc., No. 39, Ser. No. 5201: 14 p.

1978b. Age and growth of the Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), in ICNAF Subareas 2−4. ICNAF Res. Bull. 13: 5−10.

1980a. Stock assessment and abundance of Greenland hal-

ibut in the Canadian North Atlantic Subarea 2 and Divisions 3KL. NAFO Scr. Doc. 80/VI/96.

1980b. Fecundity of Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), from southern Labrador and south eastern Gulf of St. Lawrence. J. Northwest Atl. Fish. Sci. 1: 39–43.

BOWERING, W. R., AND T. K. PITT. 1975. Yield per recruit assessment of Greenland halibut (*Reinhardtius hippoglossoides*), ICNAF Subarea 2 and Divisions 3K and 3L. ICNAF Res. Doc. No. 24, Ser. No. 3479.

CHUMAKOV, A. K. 1975. Localities of Greenland halibut stocks in the north-west Atlantic. Polyarn. Nauchno Issled. Proektn. Inst. Morsk. Rybn. Khoz. 35: 203–209. (Trans. from Russian by Fisheries and Marine Service Trans. Ser. 3916)

FAIRBAIRN, D. J. 1981. Biochemical genetic analysis of population differentiation in Greenland halibut (*Reinhardtius hippoglossoides*), from the Northwest Atlantic, Gulf of St. Lawrence, and Bering Sea. Can. J. Fish. Aquat. Sci. 38: 669–677.

HARVEY, W. R. 1975. Least-squares analysis of data. Agricultural Research Service (ARS H-4), U.S. Department of Agriculture, Beltsville, MD, 157 p.

HUBBS, C. L., AND N. T. WILIMOVSKY. 1964. Distribution and synonomy in the Pacific Ocean and variation of the Greenland halibut (*Reinhardtius hippoglossoides*) (Walbaum). J. Fish. Res. Board Can. 21: 1129–1154.

KHAN, R. A., M. BARRETT, AND J. MURPHY. 1980a. Blood parasites of fish from the northwestern Atlantic Ocean. Can. J. Zool. 58: 770–781.

KHAN, R. A., J. MURPHY, AND D. TAYLOR. 1980b. Prevalence of a trypanosome in Atlantic cod (*Gadus morhua*) especially in relation to stocks in the Newfoundland area. Can. J. Fish. Aquat. Sci. 37: 1467–1475.

LEAR, W. H. 1970a. The biology and fishery of the Greenland halibut (*Reinhardtius hippoglossoides*, Walbaum) in the Newfoundland area. Master's Thesis, Department of Biology, Memorial Univ. Newfoundland, St. John's, Nfld. 132 p.

1970b. Fecundity of Greenland halibut (*Reinhardtius hippoglossoides*) in the Newfoundland–Labrador area. J. Fish. Res. Board Can. 27: 1880–1882.

LEAR, W. H., AND T. K. PITT. 1971. Distribution of Greenland halibut in the Newfoundland–Labrador area in relation to depth and temperature. Fish. Res. Board Can. Tech. Rep. 274: 34 p.

1975. Otolith age validation of Greenland halibut (*Reinhardtius hippoglossoides*). J. Fish. Res. Board Can. 32: 289–292.

MARGOLIS, L. 1963. Parasites as indicators of the geographical origin of sockeye salmon, *Onchorhynchus nerka* (Walbaum), occurring in the north Pacific Ocean and adjacent seas. Bull. Int.North Pac. Fish. Comm. 11: 101–156.

SMIDT, E. 1969. The Greenland halibut (*Reinhardtius hippoglossoides*, Walbaum) biology and exploitation in Greenland waters. Medd. Danm. Fisk. Havundersøg. (N.S.) 6: 79–148.

SNEDECOR, G. W., AND W. G. COCHRAN. 1967. Statistical methods. The Iowa State University Press, Ames, IA. 593 p.

TEMPLEMAN, W. 1970. Vertebral and other meristic characteristics of Greenland halibut, *Reinhardtius hippoglossoides*, from the northwest Atlantic. J. Fish. Res. Board Can. 27: 1549–1562.

1973. Distribution and abundance of Greenland halibut (*Reinhardtius hippoglossoides*, Walbaum) in the Northwest Atlantic. ICNAF Res. Bull. 10: 83–98.

TEMPLEMAN, W., AND A. M. FLEMING. 1963. Distribution of *Lernaeocera branchialis* (L.) on cod as an indicator of cod movements in the Newfoundland area. Int. Comm. Northwest Atl. Fish. Spec. Publ. 4: 318–322.

TEMPLEMAN, W., AND H. J. SQUIRES. 1960. Incidence and distribution of infestation by *Sphyrion lumpi* (Kroyer) on the redfish *Sebastes marinus* (L.) of the western North Atlantic. J. Fish. Res. Board Can. 17: 9–31.

TEMPLEMAN, W., H. J. SQUIRES, AND A. M. FLEMING. 1957. Nematodes in the fillets of cod and other fishes in Newfoundland and neighboring areas. J. Fish. Res. Board Can. 14: 831–897.

ZILANOV, V. K., A. A. STROGANOV, F. M. TROYANOVSKY, AND A. K. CHUMAKOV. 1976. The results of the study of commercial reserve of Greenland halibut at the continental slope in the Northwestern Atlantic. ICNAF Res. Doc. No. 109, Ser. No. 3932.

Recognition of the Possible: An Advantage of Empiricism in Ecology[1]

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In many sciences there exist unpredictable phenomena, phenomena that for one of several reasons are deduced to be unpredictable from a current paradigm theory. In ecology, the long-term abundance of a given species in an ecosystem is an example of an unpredictable variable. From the theory of the ecosystem as a highly interactive complex of species in which rare species can potentially become abundant, we can deduce that species-based, systems analysis modeling cannot make long-term forecasts of species abundance. From the theory of evolution by natural selection it can be further deduced that no theory, regardless of its structure, can make these predictions. Because our general theories are informal and often only implicit, deductions such as those I have drawn may be incorrect. Nevertheless these deductions give compelling reasons for applied ecologists to pay serious attention to our general ecological theories and their consequences. They also suggest that empirical ecologists who concentrate their efforts on predictable properties of ecosystems remain on firm theoretical grounds and are not merely avoiding the more difficult problems.

Key words: ecological theory, empiricism, prediction

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Il existe, dans bien des sciences, des phénomènes imprévisibles, qui, pour une de nombreuses raisons, sont jugées ainsi selon une théorie paradigmatique courante. Un exemple d'une variable imprévisible en écologie est l'abondance à long terme d'une espèce donnée dans un écosystème. En se basant sur la théorie que l'écosystème est un complexe d'espèces hautement interactif, dans lequel les espèces rares peuvent devenir abondantes, on peut déduire que la modélisation par analyse des systèmes, reposant sur l'espèce, ne permet pas de prévisions d'abondance à long terme. Il est en outre possible de déduire, selon la théorie de l'évolution par sélection naturelle, qu'aucune théorie, quelle qu'en soit la structure, ne peut engendrer ces prédictions. Par suite de la nature non formelle et souvent implicite de nos théories générales, des déductions telles que celles que je viens de faire peuvent être inexactes. Elles incitent cependant les spécialistes de l'écologie appliquée à se pencher sérieusement sur nos théories écologiques générales et sur leurs conséquences. Les déductions donnent également à penser que les chercheurs en écologie empirique qui concentrent leurs efforts sur les propriétés prévisibles des écosystèmes doivent s'en tenir à une solide théorie et non simplement éviter les problèmes difficiles.

ALTHOUGH the methods of science have been described and disputed for centuries there is one aspect of the sequence of scientific development that, to the particular disadvantage of ecology, has not received adequate attention. This aspect concerns the role and temporal position of empirical theory in the development of a particular branch of science. Over the last decade I have tried to defend empiricism by explaining its role (Rigler 1975a, 1975b, 1982), and have discovered more active resistance than I had expected. Consequently, I have recently turned into a defendant of empiricism (Rigler 1982). The purpose of this paper is to continue developing the case for the defense by attempting to answer a criticism of em-

[1]This article is based on a lecture given by Dr. F. H. Rigler on the occasion of receiving the first Award for Excellence of the Rawson Academy of Aquatic Science. The award was jointly presented to Dr. Rigler by Mrs. Hildred Rawson and Mr. Bruce Rawson, wife and son, respectively, of Donald S. Rawson (1905 – 1961), after whom the Rawson Academy was named. The specific citation to Dr. Rigler read: "Pioneer in elucidating the dynamics of the phosphorus cycle in lakes, integrator of part and whole, provocative thinker whose unconventional standards have helped others to find their way." The award was presented on January 6, 1982, on the occasion of the Annual Meeting of the Canadian Society of Limnologists.

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pirical ecology that I consider most important but which I have previously ignored because it is the most difficult criticism to answer.

Before proceeding to do so I must first explain what I mean by "empirical" science or "empirical" theory because I am using the term in a restrictive sense. To the philosopher, all scientific theories are empirical because they are inspired by sense data and can be falsified by comparing their predictions with new sense data. However, I want to be able to distinguish between two types of theory, both of which are scientific and, thus, in the general sense of the word, empirical. The first type, for which I retain the term *empirical theory*, is the type of theory that merely predicts the future states of a system. Often it is no more than the expression of the correlation between two state variables of the system. The second type of theory also predicts, but it goes beyond mere prediction. It purports to explain to us why the system behaves as it does and, hence, why our predictions will be valid. I call this type of theory an *explanatory theory*. Occasionally, for variation, I refer to explanatory, ecological theory as *analytical theory*, because most ecologists believe that when explanatory ecological theories do appear, they will derive from analytical studies of components of ecosystems and the interactions of these components.

The attitude I have tried to propagate is that the two types of theory, empirical and explanatory, are neither rivals nor mutually exclusive, but are both valuable aspects of science. In fact, they are complementary, in that each plays an essential role in the normal sequence of scientific advance. In a new branch of science that is characterized by the absence of predictive theories, the first advance is made by the empiricist who looks for regularities in the behavior of the systems under investigation. If he succeeds, he expresses the discovered regularities quantitatively, and by doing so has constructed an empirical theory. When one or more empirical theories exist, the scene is set for the explanatory scientist who attempts to bind the empirical theories together, or reformulate them into an explanatory theory. The essential role of empiricists is to provide the raw material with which the explanatory scientist can work.

A well-known example of an empirical theory is given by Kepler's laws of planetary motion. From these, astronomers could predict the future states of the solar system, despite the fact that Kepler's laws did not tell us why planetary bodies behave as they do. Understanding was subsequently provided by Newton who introduced the concepts of gravitation and conservation of momentum. Collectively, Newton's laws comprised an explanatory theory of planetary motion.

It should be unnecessary to preach the merits of an essential part of science, but I believe that many ecologists are unusual among scientists in that they deny the need for empirical science. This belief is hard to substantiate because, as far as I know, the role of empiricism in ecology has not been put to the vote and ecologists, unlike their more successful colleagues in physics, seem remarkably unwilling to examine the structure of their beliefs. Consequently, evidence for our beliefs can only be inferred from our behavior, and the nature of undergraduate training in ecology is a good index of our behavior. At present there is no textbook of empirical ecology and among the plethora of texts dedicated to analytical ecology, none gives a balanced account of the predictive value of empirical theories. In fact, lacking predictive explanatory theories to teach we prefer to indoctrinate our students in pseudotheory and metaphysics (Murdoch 1966; Peters 1976). Much of the illustrative detail deals with the methodology and results of analytical studies without explaining that the body of explanatory theory is a dream rather than reality.

For me, the most useful indication of majority attitude to empiricism is the nature of questions and comments elicited by a lecture on empirical ecology. I have been told that empiricisms are engineering, but not science, that empirical science is best avoided because it offers no intellectual challenge, and that it is scientifically sterile because it inevitably leads to a dead end. Comments such as these and the nature of undergraduate training in ecology suggest to me that empirical ecology badly needs advocates.

Recently (Rigler 1982) I have tried to counter some of the criticisms of empirical ecology. The purpose of this essay is to attempt to reply to the most difficult and significant objection to empiricism, the complaint that empirical ecology is of no value, despite its obvious successes, because it has failed to make the types of predictions about ecosystems that we (and society) really need.

An Unsatisfying Rebuttal

Before defending any approach to science it is essential to establish the ground rules of argument. These are very simple. Success is the only valid criterion. To evaluate an approach we ask if it has successfully generated predictive theories. To compare two approaches we must evaluate their past accomplishments. We cannot base a discussion on our faith that an approach will be successful one day. This would be tantamount to defending an hypothesis by argument rather than by experiment. Although this simple point may seem self-evident it must be made because many ecologists cling to the Baconian philosophy of science that theory is meticulously assembled out of facts as a house is assembled from bricks. From this belief it follows that the emergence of a theory will follow as inevitably from the painstaking collection of facts as the house will emerge from the bricks. Alas, this comforting philosophy has long been superceded by the recognition that theory is the product of inspiration. The analogy is false and we can never know in advance what approach will succeed.

Having reminded my critic of this ground rule, I attempt to satisfy his objection by comparing the predictive capacity of empirical ecology with that of explanatory ecology, show that the former is greater, and conclude that the critic was asking for too much. If a branch of science can be rated on a scale from zero to infinity where zero is the starting point at which we can predict nothing, and infinity is the finish where we predict everything, I say that empiricisms have taken us to one (Fig. 1) whereas explanatory ecology remains at or near zero. The critics of empiricism compare our present position unfavorably with infinity when they should be comparing it favorably with zero.

To my surprise and dismay this crushing argument never convinced any explanatory ecologist. Finally, I realized that although my answer was valid I was answering the wrong criticism. The critic never expected empirical ecology to pre-

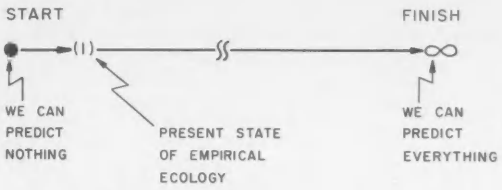

FIG. 1. Schematic representation of the current state of empirical ecology.

dict everything. He was objecting not to the quantity of predictions, but to the quality, because he perceives empirical ecology predicting the wrong kinds of state variables. (A state variable is any measurable property of the system under study.) Long ago, Elton (1927) and later Andrewartha and Birch (1954) defined ecology as the science that attempts to predict the abundance and distribution of organisms.[2] When we, as animals, look at the external world we don't see abstract state variables, we see species. When we hunt or harvest, we generally go after species, not state variables such as biomass or chlorophyll *a*. These are basic truths of life that my critic perceived and I missed. He did not mean that empirical ecology had failed because it could not predict everything about ecosystems. He meant that it had predicted the wrong types of state variables. Instead of concentrating on species abundance, empiricists have developed theories to predict components of ecosystems such as Chl *a*, total phosphorus, turbidity, or dissolved oxygen. Although Ryder's (1965) morphoedaphic index comes closer to their species-based aspirations it still only predicts the mean annual harvest of all fish and fails to distinguish between those species we want and those we do not want. From the point of view of Elton, and Andrewartha and Birch, empirical ecology has been a total failure; it predicts nothing that matters. Furthermore, to add insult to injury most empiricists do not even appear to be interested in predicting species abundance.

The purpose of this paper is to answer the reformulated criticism of empirical ecology by demonstrating that the critics have unrealistic expectations not only of empiricists, but also of themselves. My approach will be to attempt to convince the reader that some scientific phenomena are theoretically unpredictable and that the future abundance of species may be an example of this type of phenomenon.

Unpredictables in Science

Because ecologists tend to be Laplacian as well as Baconian in their philosophy of science, we rarely, if ever, consider the possibility that the tasks we set ourselves are impossible despite the fact that we continually excuse our failures by explaining that our experimental material is much more complex or less tractable than that of our successful colleagues in the physical sciences. The very idea that some ecological phenomena could be unpredictable is foreign to most of us. Therefore I will begin explaining what I mean by "unpredictable" and by showing that unpredictable events exist in a variety of sciences.

First we must clearly distinguish between events that one cannot predict and those I call "unpredictable." The former are merely classes of events not yet embraced by a functional scientific theory. For example, we cannot yet predict the ratio of total N:total P in lakes, but there is nothing in current limnological theory that tells us this ratio is essentially unpredictable. Phenomena such as this are "potentially predictable," and are definitely not the type of event that concerns me. The classes of events that I shall discuss are those that our paradigm theories tell us are unpredictable. Acceptance of such a theory therefore implies acceptance of the possibility that certain events are unpredictable in principle.

It is self-evident that although the distinction between potentially predictable events and unpredictable events is unambiguous, a given class of events may be unpredictable one year and predictable the next. Theories change and the theory that today tells us that a class of events is unpredictable may one day be rejected in favor of a theory telling us that these events are potentially predictable. Nevertheless, for the scientist working under the former paradigm theory, the events must be considered unpredictable.

Examples of unpredictable events in science are common enough that a tentative classification of them is possible. I can see four reasons why we cannot expect to succeed in making predictions about future states of a system or of particular state variables of that system: (1) the behavior of the system is random; (2) the only potential methods of obtaining information about the system disturb it; (3) the system gives out no information; and (4) the behavior of the system is affected by the theory.

Random Events

The most familiar example of a random event is the decay of an atom of a radioactive isotope. If the system comprises a large number of atoms of the isotope we can predict empirically how many will decay in a given time, but we cannot predict which ones will decay. Given a system comprising a single atom of the isotope, no physicist will attempt to predict when it will decay. The most he will do is give the probability of its decaying in a certain time. This is because current theory states that radioactive decay is a purely random process.

Despite Einstein's persistent belief that God left nothing to chance, the phenomena that gave rise to quantum mechanics are still believed to be random. Given a quantity of hydrogen excited to a high temperature we can predict exactly what wavelengths of light it will emit and how many photons of each wavelength will be emitted, but given one atom we do not attempt to predict when it will emit a photon, or what the wavelength of that photon will be. Again this is because theory states that the movement of an electron between its possible energy levels is random.

Biological theory also dictates that certain events are random, the best known being gene mutation. Given a large population of *Drosophila*, homozygous at a particular gene locus, we can predict empirically the frequency at which other

[2] In fact, both said our job was to *explain* the distribution and abundance, but because one cannot explain without predicting it was implicit in their definition that ecology should predict, as well as explain, the distribution and abundance of species.

alleles of that gene will appear in the population. However, no Mendelian geneticist would attempt to predict which of a large sample of offspring from matings of parents known to be homozygous at that locus will carry a recessive mutation. Neither would he attempt to predict which of the known recessive mutations of that allele would have appeared in any individual identified for him as a mutant. Once again the reason these phenomena are unpredictable is that theory tells us that mutations occur at random due to the chance collision of, say, a cosmic ray or mutagenic chemical and a DNA molecule.

Not surprisingly there are few examples of totally random behavior of whole organisms although in many aggregative processes stochastic elements often play an important part. One intriguing example of an apparently random behavioral phenomenon was reported by Corkum (1978) who was studying stream drift of insect nymphs. She showed that *Baetis vagans* spontaneously left the substratum and that if a large population was placed on a brick the number leaving (after an initial period of disturbance) decreased log-linearly with time. Just as with radioactive decay the probability of any individual changing its state appeared to be a constant. Confirmation of this inference as well as a search for other random processes at the whole-organism level might prove to be interesting in revealing unpredictable events at the whole-organism level.

System is Disturbed by the Experimenter

The second situation that prevents us from making specific predictions occurs when we are unable to extract from our system the information needed to initialize our calculations without seriously disturbing the system. We inevitably cause some disturbance to any system under investigation, but we accept this limitation provided the disturbance is negligible, can be corrected for, or does not introduce intolerably large confidence limits into our predictions.

The classic example of a system whose behavior is grossly altered by our measurements is the electron. Our measuring devices are necessarily so clumsy that we cannot know both the location and vectoral velocity of an electron. We can measure one or the other, but not both. Consequently we can never expect to predict the future location of our electron.

This situation is also well-known to biologists who spend a large fraction of their journal space attempting to convince their skeptical colleagues that the techniques they have applied have given a valid picture of the system behavior. Students of animal behavior are particularly concerned with this difficulty, but few of us, regardless of our field, passed through a formal training in biology without being chilled by the grey-beard who nullified our conclusions by saying, "Aha, it may have worked in the lab, but how do you know it will work in the field?" In my terminology he was really asking whether our measuring techniques had changed the system enough to invalidate our predictions.

System Yields No Information

If a system provides no measurable information it is obviously a system about which we are unable to make predictions. Systems of this type are understandably rare. By definition we can do no more than postulate their existence and deduce their properties from theory or from some intuitive first principle. Astronomy has generated one system of this type, the singularity at the center of a black hole. Because theory tells us that the singularity neither reflects nor emits any particles or waves we cannot experiment with it. It is a system that is beyond science (unless one day we can call anti-matter into service as a measuring device).

Biology possesses the best known example of an inaccessible system in the human soul. By definition the soul is immaterial and cannot be detected by any physical or chemical techniques. Consequently scientific predictions about the future states of a soul are impossible. However, despite its similarity to the singularity, the soul does not conform to my requirements for an unpredictable system, because its existence derives not from scientific theory, but from theology, and unpredictables can only be deduced from currently accepted scientific theory. If a new general physiological theory from which we can deduce the existence of a soul is introduced and becomes generally accepted, then the soul will be elevated to the status of the singularity, and if the deduced soul still has no measurable properties we will be able to think of it as another truly scientific unpredictable.

System is Affected by the Theory

This problem arises in theories about systems comprising human beings in addition to other living and nonliving components and consequently is of greatest concern to theorists in subjects such as history, sociology, and economics. The problem arises because the behavior of human beings is affected by book learning. In effect, any newly accepted theory becomes part of the system about which predictions are to be made. Therefore, introduction of a new theory effectively eliminates the old system and replaces it with a new one. Consequently sociologists and economists can only be expected to predict those state variables that are common to all possible human societies from theories that are somehow independent of the state of human knowledge. This is a serious and perhaps insurmountable difficulty that may explain the remarkable failure of disciplines involving human society to achieve the predictive theories that would have earned them a place among the hard sciences. Although this interesting limitation of science impinges on ecology via the management strategies for economic resources (Larkin 1979), it, as well as the system that yields no information, will not be discussed here in relation to the difficulties of predicting the future abundance of species.

Unpredictables in Ecology

Now that I have shown that there are categories of unpredictable phenomena in fields other than ecology, the reader should be better prepared to contemplate the possibility that there are examples of unpredictables in ecology itself. I will now attempt to demonstrate that the future abundance of any species is one of these and that this conclusion is deducible from two widely accepted theories.

Before doing so, I must qualify the term "future abun-

dance." What we really need to predict are the long-term effects of proposed management techniques or of a variety of anthropogenic stresses on whole ecosystems or individual species within these systems. For example, what will be the overall effects on species in the system by changing the catch limit or minimum age of a harvested species? How will the abundance of important species in a system be affected by the addition of a new pollutant such as a heavy metal, or acid, or heat? These are the kinds of questions that environmental impact assessments are expected to answer. By "long-term" I mean periods as long as or greater than the human life span. Short-term changes in the abundance of species are often easily predicted from simple empirical generalizations or population statistics. Aristotle knew that plagues of mice occurred in dry seasons and we can now predict when locusts or spruce budworm will be abundant and even when a large year-class of some aquatic species will appear (Sutcliffe 1973; Stevens 1977; Orth 1979). I am neither discussing these short-term predictions, nor the relatively trivial predictions we can make about pairs of tightly linked species such as a parasite and its host or an obligate stenophage and its food species. In cases such as these no sophisticated theory is needed to predict the abundance of the parasite or predator if the host or prey becomes extinct. Our concern is to develop theories that will predict for years into the future the abundance of species that are part of the food web of an ecosystem and this is the type of prediction our current paradigm theories of the ecosystem and evolution deny us.

Difficulties Deriving from Ecosystem Theory

Definition of the Theory

Scientific theories vary greatly in sophistication. At best a theory can be highly formalized and quantitative; at the other extreme it can be very vague and unquantitative. Our theory of the ecosystem is difficult to define because it is near the latter end of the spectrum. I think this situation persists because we ecologists have been slow to draw analogies between the methods of the mature sciences and of our own. In particular we were slow to answer the most fundamental question of any embryonic science. What is the system with which we must work? This question is critical because the system is equivalent to the class of objects about which we will construct our theories. Ecologists effortlessly eliminated the individual organism as a useful system; it was too obviously subject to random events. However, there was a strong tendency to adopt the population as our system. Although this was only temporarily satisfying, some ecologists, such as fisheries managers, persisted to retain it for decades (Larkin 1977; Rigler 1982). But most ecologists have long, uneasily acknowledged that the population is not an isolated system controlled only by physical and chemical variables. Evidence for the predominant effect of species–species interactions has overwhelmed us for generations. Hence we accepted Evans' (1956) advice to use the ecosystem as the basic system of ecology and, having also accepted the predominance of intricate food webs over the simplistic food chain, we pictured the species within the system being highly interactive.

The process of enlarging our basic system did not stop here. Recognizing that there are interactions between adjacent ecosystems some ecologists, particularly limnologists, have expanded their system to include an entire drainage basin, whereas environmentalists concerned with the future of our species treat the entire biosphere as their system. Despite the possible merits of these further enlargements, the problem that concerns me is adequately explained by taking the traditional ecosystem as the basic system for ecological theory.

For my argument it is the consequences of accepting the current view of the ecosystem that are important. This view reduces the population to one state variable of the ecosystem in which it occurs. Thus the future abundance of one species in an ecosystem cannot be predicted from a theory that does not also predict the abundance of all other coexisting populations. All are interrelated by a web of intense interactions in which the abundance of one species may be influenced by that of any other species.

Perhaps because we saw no way of dealing with this apparently intractable situation many of us deluded ourselves that description, not prediction, was our goal. Alternatively some of us ignored the implications of accepting the ecosystem as the basic unit of study (Rigler 1975a). Finally, the development of computers and systems analysis appeared to offer an escape from our dilemma. The solution appeared to be to use a *species-based system analysis model* of an ecosystem to predict the future abundance of populations in that system. Although acceptance of *species-based systems analysis modeling* (SAM) by ecologists is far from universal it is the only approach that acknowledges our picture of the ecosystem comprising a highly interactive complex of species. This is why I have chosen to show that SAM is theoretically incapable of predicting future abundance of species, at least until we revise our theory of the ecosystem.

Introduction to SAM

Systems analysis is merely a method of modeling the behavior of a complex system with inputs, outputs, and comprising many interacting components or subsystems. To initialize the model every component of the system, whether it be a specific compound in a chemical factory or the population of a species in an ecosystem, must be quantified. (If the system has only one potential equilibrium condition with the given inputs and outputs, the components need not be quantified.) In an ecosystem the components do not need to be species; they can be any recognizable subsystem we choose, but if the model is to be used to predict abundance of species, the components obviously must be species or subsets of these such as age-classes of species. It is important to remember that *every interacting component of the system must be included in the model* (Watt 1966).

Next, all processes causing each component of the system to grow or shrink must be identified. In ecosystem modeling one normally focuses on the flow of energy or material between species. To visualize the model we usually picture each component as a box and indicate the flux of energy into and out of the component by arrows (Fig. 2). These fluxes are variable because each will be influenced by the size of the donor and receiver populations as well as by the integrated

FIG. 2. The subsystem of an ecosystem SAM.

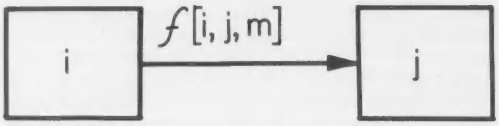

FIG. 3. The form of the interaction between two subsystems.

effect of all environmental variables. These environmental variables I will call "modifying" factors rather than use Fry's (1947) familiar "limiting, controlling, and lethal" factors because the emphasis here is on factors as they modify the flux of energy between populations rather than on factors affecting the activity of an organism.

The interaction between two components (i and j) of the system can be visualized as in Fig. 3 where $f[i,j,m]$ is a complex function influenced by the abundance of i, the abundance of j, and by all modifying factors (m). To complete the formulation of the SAM, this complex function must be constructed for each pair of interacting components in the system.

With this brief introduction to SAM we can deduce the theoretical objections to SAM, but first I will briefly describe two generally recognized objections to SAM deriving from practical problems. My objective is to contrast the practical with the theoretical problems to show that the well-known practical problems, although important, are relatively trivial compared with the theoretical objections to SAM.

Practical Problems with SAM

The first practical problem is caused by the large number of species inhabiting most ecosystems that interest us. For example, a temperate lake might support 1000 species. If each species interacted with every other species we would have $(1000 \times 999)/2$, or $\sim 0.5 \times 10^6$ potential interactions to investigate. Each potential interaction must be demonstrated to be insignificant or quantified. If we estimate an effort of one man-year per potential interaction it would take half a million man-years to gather the data required for one systems analysis model. Because this is much in excess of any effort we have previously conceived, even for large-scale cooperative projects such as the International Biological Programme, it is tempting to rule out SAM as a feasible approach simply because it requires too much work. However, I do not believe we should be convinced by this type of argument. If we desperately need predictions and believe that an approach will yield those predictions, then we should be able to marshall and direct an enormous amount of biological effort that is currently dissipated on a variety of small, independent studies.

The second practical problem is merely an extension of the first. By definition the species-based systems analysis model is system-specific unless we have two or more systems with the same complement of species. Consequently much of the effort that went into the first systems analysis model will be repeated in succeeding models. Again this system specificity makes SAM impractical. Nevertheless, I do not believe this presents an insuperable objection to SAM either, because the workload would decrease with each SAM and if our first were successful we would be more willing to embark on the second.

I have raised these objections only because they are commonly voiced by opponents of SAM. Personally I think they are insignificant in relation to the theoretical objections to SAM that I will now raise.

Theoretical Objections to SAM

The first theoretical problem with SAM arises from the general, simple relation between the rank and abundance of a species in an ecosystem (see Williams 1964 for examples). The result of this relation is that excluding very small samples, the number of species we find in a system increases continuously with the area sampled according to the equation:

$$\text{no. of species} = k \times \ln(\text{area sampled})$$

The consequence of this relation for the systems analysis modeler is obvious, because his first chore is to identify all components of the system he intends to model. It tells us that he cannot do this by taking a small sample from the system to be modeled because it would miss many species. But it also tells us that he cannot discover every species without making the sample size equal to the entire ecosystem. Thus, the first step in SAM destroys, or at least totally changes the system. In other words there will always be a large uncertainty associated with any species-based systems analysis model because the closer we come to gathering the required data, the more we change the system under study. Heisenberg would be very sympathetic.

The apparent escape from this dilemma is simply to ignore all rare species and omit them from the model, but although this expedient has obvious practical advantages, it does not overcome the theoretical objection based on our existing model of the ecosystem. It merely revises our ecosystem theory to state that rare species are not part of the ecosystem and furthermore that under no circumstances can a rare species become abundant. Unfortunately this revision of the theory is unlikely to be generally accepted, even in the improbable event that the rarest species could be demonstrated not to be part of the system, because we have a plethora of examples of rare species becoming common when environment changes. Lake Washington alone provided two good examples, first the sudden massive appearance of *Oscillatoria rubescens* during its eutrophication and then the appearance of *Daphnia* during its restoration (Edmondson et al. 1956; Edmondson and Arni 1982).

Theoretical objections to SAM are not limited to discovering a system's complement of species. Even if this were possible the next job would be to identify and quantify all interactions between species. Unless an unforeseeable meth-

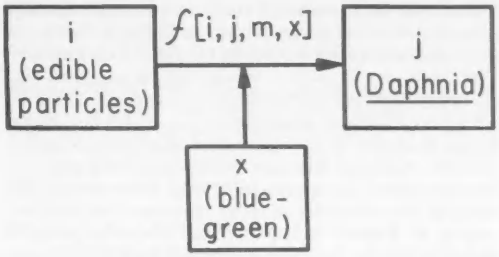

FIG. 4. Example of a third subsystem (x) affecting the interaction between two subsystems.

odological breakthrough occurs much of this work will continue to be done with isolated pairs of species in the laboratory where we can vary the physical–chemical variables and the density of the two species independently. There would be no theoretical objection to this procedure, provided none of the other components of the ecosystem affects the interaction between the two isolated species, but there are too many examples of this phenomenon for us to ignore its existence.

To show what I mean by a third component of the system acting directly on the interaction between another pair of components, I will give two examples, both from studies of zooplankton feeding behavior. In the first, Carolyn Burns (1968) working with *Daphnia* feeding in natural mixtures of phytoplankton showed that certain blue-greens are not eaten by *Daphnia*. Nevertheless they are collected by the filtering apparatus only to be subsequently rejected when they touch the *Daphnia*'s labrum. Because the rejection mechanism is nonselective, a bolus of perfectly acceptable food cells is frequently rejected with the offensive blue-green colony. Consequently good food is wasted and the blue-green by its presence affects the energetics of food collection by *Daphnia* although it is not a food species. It is a third system component affecting the interaction between another pair (Fig. 4) and it effectively adds another level of complexity (x) to the flux function that would have gone undetected in a two-component study.

The second example is from the work of Karen Porter (1976) who showed that some species of algae that are ingested by *Daphnia* are neither digested nor harmed while passing through the *Daphnia* gut. More important, it appears that they profit by exposure to the higher PO_4 concentration inside the gut. In this case the primary interaction in question is the uptake of PO_4 by the indigestible algal species and the third component impinging on the interaction is the zooplankter (Fig. 5).

Both examples show that with the methods currently available to us it is theoretically impossible to define the primary interaction between ecosystem components and hence to build a reasonably predictive systems analysis model. They provide another example of our experimental approach changing the system for which we want to construct a predictive theory. The pairs of components cannot be studied in isolation because isolation destroys their role as system components. In this case it is harder to imagine any modification of ecosystem theory that could eliminate the problem although it could be

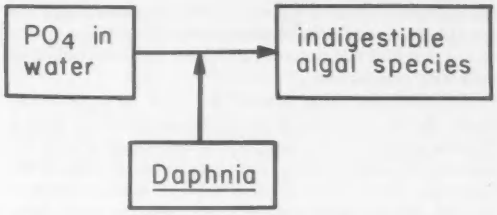

FIG. 5. A second example of one subsystem affecting the interaction between two others.

relegated to a methodological rather than a theoretical limitation if only we could conceive of practical methods of varying species density and physical–chemical conditions independently in the intact ecosystem. Also I confess that there is nothing novel about this particular objection to SAM. It is no more than a restatement in terms of SAM of the century-old objections that organicists made to the methods of the (then) physiological reductionists. Although confident methodological reductionists now seem to be predominant among outstanding biologists and philosophers of science (Goodfield 1972), this confidence may be less justified in ecology when our emphasis shifts from the description of ecosystem state variables to their prediction.

In summary, I have attempted to demonstrate that in addition to the purely logistic problems of producing a predictive systems analysis model there are two theoretical objections to using SAM approach to predict the future abundance of species. If all ecologists accepted SAM as the method of predicting future abundance of species this would be an appropriate point to end my argument. But because SAM has so far succeeded in generating little more than promises of success it has not surprisingly failed to achieve paradigm status among ecologists. For those remaining skeptical of SAM, a demonstration of its theoretical futility would not achieve my primary objective of casting doubt on the possibility of predicting the future abundance of species. Therefore I will conclude by sketching the outline of another theoretical objection to predicting species abundance derived from the more generally accepted theory of evolution by natural selection.

The Problem Deriving from Evolutionary Theory

Our current theory of evolution by natural selection tells us that any given species can be pictured not only as an assemblage of morphologically similar, potentially interbreeding individuals, but also as a gene pool. We can define a species or population at any point in time by specifying the frequency of each allele in its gene pool. (The fact that this might be prohibitively difficult to do in practice is not relevant to the argument.) The effect of natural selection is to change the frequency of some or all of the alleles in the gene pool.

Although it is possible that under constant environmental conditions conflicting selective pressures will maintain the gene pool in a reasonably steady state, a variety of influences can disturb the steady state. Among these could be the random appearance of an advantageous mutant allele, the immigration of a new species into the ecosystem, or merely a change in the

anthropogenic stresses applied to the ecosystem. Once the gene pool of one species has changed significantly, the effects of this change could cascade throughout the gene pool of all coexisting populations.

The theoretical implications of this aspect of evolutionary theory for the feasibility of predicting the effects of anthropogenic stresses on the long-term abundance of species are serious. The consequence of any stress will be a change in the gene pool of one, many, or all populations in the ecosystem. It is this change that theoretically precludes any theory from predicting species abundance regardless of the structure of the theory. The populations that exist after the change are not the same populations that existed when the theory was constructed. Furthermore the theory of evolution cannot help by predicting the nature of these changes and even suggests that many will be unpredictable.

It is an essential property of any scientific theory that the entities (concepts, state variables, etc.) that appear in the theory bear a one-to-one relation with the operationally defined entities that we can measure. By electing to build species into our theory we have chosen to use a set of ecosystem state variables that correspond to measurable variables only at the time the theory is constructed. The theory of evolution tells us that this one-to-one relation will last only until some external variable disturbs the steady state of the gene pools. In other words we have chosen to try to predict just that set of state variables that the theory of evolution tells us to be unpredictable. If we hope to predict successfully we must choose a set of state variables that will remain state variables of the changed system.

Implications for Critics of Empiricism

The general conclusion I have drawn is that several deductions from current ecosystem and evolution theory force us to accept that the long-term abundance of species in systems subject to anthropogenic or other changes is not predictable. Our current theory of the ecosystem as a highly interactive system of all species, no matter how rare, and in which at least some rare species can potentially become abundant, precludes species prediction by SAM. This is because we seriously disturb the system by gathering data necessary to construct and initialize the model. Furthermore the theory of evolution by natural selection tells us that the species is an unsuitable choice of state variable because species are transient state variables. This would not necessarily be an insuperable problem, were it not that evolutionary theory says that the changes in species are largely unpredictable because they result from random events.

The consequence of these conclusions is that any criticism of empirical ecology for its failure to produce empirical theories predicting species abundance is invalid. A branch of science cannot be faulted for failing to predict the unpredictable. Furthermore, the empiricist, by attempting to predict nonevolving state variables such as total phosphorus in lake water, chlorophyll *a*, dissolved O_2 in the hypolimnion, or sustainable fish harvest of a lake is actually behaving more scientifically than the species-based ecologist hoping to predict species abundance. This is why the empiricists have had some success. They have recognized the limits of the soluble (Medawar 1967).

Attacks on the conventional wisdom of a science frequently generate nothing but antagonism and pessimism and although intellectual antagonism is generally fruitful, pessimism is not. Therefore I want to conclude by asserting my own belief that my thesis should not be interpreted as being pessimistic. I do not believe that future abundance of species will necessarily remain an unpredictable because there are no absolute unpredictables in science. They are only deduced from currently accepted theory. The theories from which I drew conclusions about the unpredictability of species abundance are both susceptible to rejection or improvement. Ecosystem theory is particularly weak. In fact the existence of a paradigm theory of the ecosystem could be questioned. I was actually forced to formulate the theory to conform to my interpretation in order to draw deductions from it. Thus we might profit more by formalizing our theory of the structure of the ecosystem and devising methods of testing our theory than by agonizing over deductions from one version of our current theory. We should also devote more effort to deciding if the ecosystem really is the basic system of ecology and, if so, what are the most tractable state variables of this basic system. These are century-old problems that were recognized by a few ecological pioneers, but dismissed by the majority of us as irrelevant to the practical ecologist because they were too easily labeled philosophical. What I have shown is that these problems cannot be relegated to the philosopher. They are of immediate concern even to the practical environmental manager. Only by developing an unambiguous theory about the basic system in ecology will we know which of our practical problems are soluble and which are theoretically insoluble.

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ANDREWARTHA, H. G., AND L. C. BIRCH. 1954. The distribution and abundance of animals. Univ. of Chicago Press, Chicago. 782 p.

BURNS, C. W. 1968. Direct observations of mechanisms regulating feeding behaviour of *Daphnia* in lakewater. Int. Rev. Gesamte Hydrobiol. 53: 83–100.

CORKUM, L. D. 1978. The influence of density and behavioural type on the active entry of two mayfly species (Ephemeroptera) into the water column. Can. J. Zool. 56: 1201–1206.

EDMONDSON, W. T., G. C. ANDERSON, AND D. R. PETERSON. 1956. Artificial eutrophication of Lake Washington. Limnol. Oceanogr. 1: 47–53.

EDMONDSON, W. T., AND H. L. ARNI. 1982. *Daphnia* in Lake Washington. Limnol. Oceanogr. 27: 272–293.

ELTON, C. 1927. Animal ecology. Sedgwick and Jackson, London. 209 p.

EVANS, F. C. 1956. Ecosystem as the basic unit in ecology. Science (Washington, DC) 123: 1127–1128.

FRY, F. E. J. 1947. Effects of the environment on animal activity. Univ. Toronto Stud. Biol. Ser. 55. 62 p.

GOODFIELD, J. 1972. The problem of reduction in biology. Nature (London) 240: 446–448.

LARKIN, P. A. 1977. An epitaph for the concept of maximum sustained yield. Trans. Am. Fish. Soc. 106: 1–11.

1979. Maybe you can't get there from here: a foreshortened

history of research in relation to management of Pacific salmon. J. Fish. Res. Board Can. 38: 98–106.

MEDAWAR, P. B. 1967. The art of the soluble. Methuen, London. 160 p.

MURDOCH, W. W. 1966. Community structure, population control, and competition — a critique. Am. Nat. 100: 291–226.

ORTH, D. J. 1979. Computer simulation model of the population dynamics of largemouth bass in Lake Carl Blackwell, Oklahoma. Trans. Am. Fish. Soc. 108: 229–240.

PETERS, R. H. 1976. Tautology in evolution and ecology. Am. Nat. 110: 1–12.

PORTER, K. G. 1976. Enhancement of algal growth and productivity by grazing zooplankton. Science (Washington, DC) 192: 1332–1334.

RIGLER, F. H. 1975a. The concept of energy flow and nutrient flow between trophic levels. *In* W. H. van Dobben and R. H. Lowe-McConnell [ed.] Unifying concepts in ecology. Dr. W. Junk B.V., The Hague. 302 p.

1975b. Nutrient kinetics and the new typology. Int. Ver. Limnol. Verh. 19: 197–210.

1982. The relation between fisheries management and limnology. Trans. Am. Fish. Soc. 111: 121–132.

RYDER, R. A. 1965. A method for estimating the potential fish production of north-temperate lakes. Trans. Am. Fish. Soc. 94: 214–218.

STEVENS, D. E. 1977. Striped bass (*Morone saxatilis*) year class strength in relation to river flow in the Sacramento – San Joaquin Estuary, California. Trans. Am. Fish. Soc. 106: 34–42.

SUTCLIFFE, W. H. JR. 1973. Correlations between seasonal river discharge and local landings of the American lobster (*Homarus americanus*) and Atlantic halibut (*Hippoglossus*) in the Gulf of Saint Lawrence. J. Fish. Res. Board Can. 30: 856–859.

WATT, K. E. F. 1966. The nature of systems analysis, p. 1–13. *In* K. E. F. Watt [ed.] Systems analysis in ecology. Academic Press, New York. 276 p.

WILLIAMS, C. B. 1964. Patterns in the balance of nature. Academic Press, London, New York. 342 p.

Aquarium Systems. *Edited by A. D. Hawkins. Academic Press, London. 1981. x + 452 p. $67.*

The breadth of coverage in this book is unique; different researchers have provided concise reviews of every aspect of captive maintenance of fishes, such as mechanical systems and water quality, capture and handling of fish, nutrition, disease, stress, and types of specialized husbandry. The book includes 15 chapters with separate referencing, a large appendix of tables, and a subject index. The editing is excellent conceptually and the level of coverage and writing style is consistent among authors, so that a diverse audience will be well served.

For the most part, literature referencing is selective but should provide a sound beginning for detailed searches of particular subjects. Because some topics would involve too much detail for adequate coverage in such a general text, the authors have virtually omitted certain subject areas in deference to more specialized reference texts. Thus, the chapter on diets for captive fishes refers the reader to Halver (1972) for information on vitamin requirements. Similarly, the chapter on disease gives few details on systemic infections, citing Roberts (1978) as a preferred review. This editorial approach allows better balance and easier reading for such important chapters as those on fish nutrition and infectious disease.

The various chapters on physical systems and water quality seem directed at research laboratories with medium-sized systems. The one chapter devoted to small, closed aquaria is rather superficial, so that a gap exists in this book regarding practical details of small, closed systems. For the purposes of understanding and modifying designs for home aquarium systems or small, closed laboratory systems, the practical detail and attention to recent technology in Spotte's books (1979a, b) remain desirable in comparison with this text. At the other end of the size scale, designers or engineers planning major seawater systems, as for oceanariums, will find aspects of this book somewhat archaic. For example, pressure diatomaceous earth (d.e.) filtration is described in this text, whereas a modern oceanarium would have vacuum d.e. filters specified in their design. One other aspect of this book's coverage of physical systems is an almost exclusive emphasis on use of subsand infiltration beds for seawater system intakes. Subsand intakes are frequently used in Britain, but are uncommon in North America. This underscores the British background of this book and most of its authors.

That there are so many British authorities on aquarium systems is a testament to the level of research effort in that nation. Undoubtedly, however, an equally qualified text of different emphasis could emerge from experts in Japan, for instance. In most chapters, as with Blaxter's on rearing larval marine fishes or Walne's on shellfish culture, the many details of British research and commercial mariculture efforts are exemplary of advances throughout the world. In others, such as the chapter on subsand intakes, the coverage is less global. Thorpe's coverage of rearing salmonids in freshwater openly emphasizes specialized approaches used on Atlantic salmon, *Salmo salar*, with little attention to the *Oncorhynchus* species (Pacific salmon). All of the authors, however, write clear, explanatory accounts which will enable the reader to adapt information from this book to his own specialized purposes.

Research specialists will find the breadth of this text enlightening. It should be required reading for aquarists in commercial aquaculture facilities, marine research laboratories, and oceanariums. This book will probably become a standard reference text and I hope it will go through additional printings. There are minor editorial flaws in this first printing and considering the high price, a new edition in a less-expensive format would help bring this useful book within the means of students, hobbyists, and more casually interested scientists. It is important for this book to reach a wide audience because the comprehensive information it provides is essential not only to the provision of viable organisms for experimental research but also to the humane treatment of all fishes in captive situations.

HALVER, J. E. [ed.] 1972. Fish nutrition. Academic Press, New York, NY. 713 p.

ROBERTS, R. J. [ed.] 1978. Fish pathology. Bailliere Tindall (Cassell Ltd.), London. 318 p.

SPOTTE, S. 1979a. Fish and invertebrate culture: water management in closed systems. 2nd ed. J. Wiley and Sons, New York, NY. 179 p.

1979b. Seawater aquariums: the captive environment. John Wiley and Sons, New York, NY. 413 p.

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(R415)

Books Received/Livres reçus[1]

May/mai 1982

English, French and Scientific Names of Pacific Fish of Canada (Noms français, anglais et scientifiques des poissons de la côte du Pacifique du Canada). *Yves Jean, Alex E. Peden, and Don E. McAllister. Heritage Record No. 13, British Columbia Provincial Museum. 1981. 51 p.* Text in English and French; bibliography included. This publication provides a revised species list and classification of fishes within the 200-mile limit of the Pacific coast of Canada and at weathership station Papa. About 50 new records are added to the last faunal work *Pacific Fishes of Canada* for a total of 386 species. [R431]

The History of Modern Whaling. *Arne Odd Johnsen and J. N. Tonnessen. University of California Press, Berkeley. 1982. 798 p. $45 (U.S.).* This comprehensive account of modern whaling was condensed and translated from a four-volume Norwegian original. It charts the progress of the modern industry from its beginnings to the battles which continue today over regulation and national quotas. The narrative is supported by a formidable array of tabulated statistics. [R432]

Kuwait Bulletin of Marine Science. Number 2. Proceedings of the International Shrimp Releasing, Marking, and Recruitment Workshop, 25–29 November 1978, Salmiya, State of Kuwait. *Edited by A. S. D. Farmer. Kuwait Institute for Scientific Research, Mariculture & Fisheries Department, Salmiya, Kuwait. 1981. 415 p.* Probably the first publication of this type to appear in English; similar publications are available in Japanese. The workshop considered fisheries management issues, particularly the ailing fisheries of the Arabian Gulf. [R433]

Functional Adaptations of Marine Organisms (Physiological ecology series). *Edited by F. John Vernberg and Winona B. Vernberg. Academic Press Canada, Don Mills, Ontario. 1981. 347 p. $51.35.* This treatise examines functional adaptations of various organisms to foreign substances, dredging, offshore drilling, and overfishing. The chapters are ecologically oriented. Written for both marine and nonmarine scientists this book considers the functional ploys that diverse species from markedly different habitats utilize to survive and reproduce. [R434]

Principles of Benthic Marine Paleoecology. *Arthur J. Boucot, with contributions on bioturbation, biodeposition, and nutrients by Robert S. Carney. Academic Press Canada, Don Mills, Ontario. 1981. 463 p. $86.45.* This book deals with the paleoecology of the shallow-water marine environment, emphasizing those aspects of both ecology and paleoecology considered to be useful for reconstructing the continental shelf, shallow-water environments richly represented in the fossil record. The author has followed an analytical approach and suggests how the manifold variables operating in the benthic marine environment can be recognized and how the intensity of their effort could be measured in individual situations. [R435]

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[1]Persons interested in reviewing books in this list should contact the Book Review Editor, Canadian Journal of Fisheries and Aquatic Sciences, Scientific Information and Publications Branch, Department of Fisheries and Oceans, Ottawa, Canada K1A 0E6.

[1]Les personnes intéressées à examiner les livres énumérés dans cette liste sont priées de communiquer avec le Rédacteur des comptes rendus, Journal canadien des sciences halieutiques et aquatiques, Direction de l'information et des publications scientifiques, Ottawa, Canada K1A 0E6.

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Homing by Canada's west coast herring to management units and divisions as indicated by tag recoveries **A. S. Hourston**

Relationship between thickness of daily growth increments in sagittae and change in body weight of sockeye salmon (*Oncorhynchus nerka*) fry **K. H. Wilson and P. A. Larkin**

Otoliths of chinook salmon (*Oncorhynchus tshawytscha*): daily growth increments and factors influencing their production **J. D. Neilson and G. H. Geen**

Carbon inputs to bivalve mollusks: a comparison of two estuaries **L. S. Incze, L. M. Mayer, E. B. Sherr, and S. A. Macko**

Spawning behavior and early life history of pink salmon (*Oncorhynchus gorbuscha*) in the Great Lakes **W. Kwain**

A model for predicting Pacific herring (*Clupea harengus pallasi*) spawn density from diver observations **J. F. Schweigert and D. Fournier**

An evaluation of the wet oxidation technique for use in determining the energy content of seston samples **R. I. E. Newell**

Problems of species identity in the Lake Ontario sculpins, *Cottus bairdi* and *C. cognatus* **C. M. Godkin, W. J. Christie, and D. W. MacAllister**

Sublethel toxicity of cyanide to rainbow trout (*Salmo gairdneri*) at different temperatures **T. G. Kovacs and G. Leduc**

Reproductive strategy of dwarf and normal Arctic charr (*Salvelinus alpinus*) from Vangsvatnet Lake, western Norway **B. Jonsson and K. Hindar**

Measurements of growth and consumption of sauger (*Stizostedion canadense*): implication for fish energetics studies **J. W. Minton and R. B. McLean**

Temperature and scale size errors in the use of [^{14}C]glycine uptake by scales as a growth index **C. M. Smagula and I. R. Adelman**

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Acute toxicity of cyanide to rainbow trout (*Salmo gairdneri*) acclimated at different temperatures **T. G. Kovacs and G. Leduc**

Letters and Comments/Lettres et commentaires: Comment on "Multivariate analysis as a means of comparing growth in fish" **R. K. Misra;** Reply **D. R. Bernard**

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